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THE BIOLOGY OF BIRDS

PLATE I



GUILLEMOT'S EGGS, SHOWING FIVE OF THE MANY
COLOUR-VARIETIES.

About half natural size.

// THE BIOLOGY OF
BIRDS /

[Faint handwritten scribble]

BY

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PREFACE

THE aim of this book, like that of the others in the series, is to illustrate biological ideas in reference to a particular group or class of animals. In this case the selected class is that of birds, and the book applies to these fascinating creatures such biological concepts as adaptation, struggle, sex, heredity, variation, selection, and behaviour.

There are many students of birds who are expert along particular lines, having, for instance, a personal familiarity with British birds and their ways, or an accurate knowledge of birds' bones or birds' eggs, or a detailed acquaintance with what is known in regard to distribution, migration, and the nature of the food, or a quite remarkable eye for flight, and ear for song. We have had the pleasure of learning much from some of these experts, a pleasure all the greater because the lover of birds is usually a delightful person to meet; perhaps we shall not be misunderstood if we say that this book is an attempt to unite all the specialisms in an amalgam of biological ideas.

For those who have the good fortune to be nearer the beginning than the end of their studies, our book may be, we hope, of use in suggesting the length and breadth, the depth and height of the Biology of Birds.

UNIVERSITY OF ABERDEEN,
Spring, 1923.

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THE BIOLOGY OF BIRDS

CHAPTER I

THE CHIEF CHARACTERISTICS OF BIRDS

§ 1. Intensity of Life in Birds. § 2. Running and Parachuting before Flying. § 3. Supply of Body with Arterial Blood Exclusively. § 4. Warm-bloodedness. § 5. Feathers. § 6. Adaptations Accessory to Flight. § 7. Mentality of Birds. § 8. Nesting. § 9. Migration.

To say that birds are feathered bipeds is certainly to define them off from all other animals, but it leaves much to be said. Even when we add two other words and make the compact definition "warm-blooded, oviparous, feathered bipeds," there is not more than a suggestion of the singularly attractive reality. It is impossible to get the picturesque impression, which is at least part of the truth, without more details. Let us attempt an introductory statement of the salient characteristics of birds.

§ 1. INTENSITY OF LIFE IN BIRDS

Instead of beginning with feathers and flight, it may be possible to get further back and recognise the bird as a creature of intense metabolism. This, we think, is the heart of the matter, that whereas reptiles are on the whole slow-going, the bird that arose millions of years ago from one of the reptilian stocks diverged in the direction of living much more nearly up to its income. Its constitution was geared to a higher rate than that of reptiles. This seems to have been an ever recurrent dichotomy in evolution, a separation of the slow-goers from the quick-goers,

of the careful from the adventurous. Not that it was necessarily a dichotomy, for at many a level in the genealogical tree, we seem to see a trifurcation, rather than a bifurcation. Between the extremes of great activity and great passivity, others found a *via media*.

“Living more nearly up to income” may sound metaphorical, but what is meant is that the ratio of disruptive, down-breaking processes (katabolism) to constructive, up-building processes (anabolism) is high in the bird’s constitution. In every viable body the fraction $\frac{A}{K}$ must always be greater than unity; in the bird the denominator is large. Continual oxidation or combustion of carbohydrate material is needed to keep the muscles, we shall not say “contracting,” but “able to continue contracting.” The bird’s breathing is very rapid. The heart beats very quickly. The blood is astonishingly rich in red blood-corpuses. The bird is selective in its diet, rarely eating much that is unprofitable, and it makes the most of its food, for the digestion is singularly perfect, as may be seen in the relatively small amount of faecal matter. It takes millennia to make a guano deposit, and the guano is mostly from the kidneys, not from the food-canal of birds. In general, then, the bird is a high-gearred engine. That is evident from the high temperature, which is from 2° to 14° F. higher than that of mammals.

§ 2. RUNNING AND PARACHUTING BEFORE FLYING

Given a spare muscular type of body, good breathing, a strong heart, perfect digestion, and rich blood, it is natural to expect active habits—running, jumping, climbing, and parachuting from tree to tree. An examination of a bird’s wing shows, in varied development, a web or skin (patagium) extending from the shoulder-joint along the upper or pre-axial margin of the arm (see Fig. 17). It is possible that this was the incipient wing with which primitive birds started, and that they raced along the ground as bipeds, taking occa-

sional skimming leaps, helped by strokes of the somewhat webbed fore-limbs and balanced by the outstretched tail. It is more than a guess that birds had to walk as bipeds before they could run, and that they had to leap before they could fly. For the palæontological facts, to be discussed afterwards, point to the extinct Dinosaurs as the stock from which birds evolved, and point particularly to a sub-order known as the Ornithischia, some of which were bipeds. Thus there is a basis of fact for the view that the primitive birds were bipeds before they were fliers. It is interesting to find in the Australian Collared Lizard (*Chlamydosaurus*) an animal which at the present day is making essays in bipedal progression. It runs a short distance almost erect, and then topples down on all fours again. After a period of terrestrial life, birds became no doubt arboreal, and after a period of arboreal apprenticeship in which the fore-limbs were mainly used as parachutes they acquired true wings—striking the air. The point to be considered is that the assumption of a bipedal mode of progression, indicated by the extinct Ornithischia, implied an emancipation of the fore-limb from the task of being a supporting organ, and opened up the possibility of a new function, namely, flight.

§ 3. SUPPLY OF BODY WITH ARTERIAL BLOOD EXCLUSIVELY

It is not a wild fancy to suppose that before birds were fliers they had acquired a four-chambered heart and other arrangements that secured a supply of nothing but arterial blood to the body. For that would mean a raising of the pitch of the whole life. Here it must be remembered that in most reptiles there is an incomplete septum up the middle of the driving chamber or ventricle of the heart, so that the impure blood which comes in from the body *via* the right auricle is not completely shut off from the pure blood which comes in from the lungs *via* the left auricle. It is not a very big anatomical advance to have this ventricular

septum completed, and it is completed in crocodilian reptiles. But although the crocodile has a four-chambered heart, it does not, so to speak, make the best of it, for the blood that goes to the posterior body is mixed blood (the dorsal aorta being formed by the union of a right aortic arch with pure blood, and a left aortic arch with impure blood). In birds the aortic arch which gives off the blood-vessels to the head, and is turned round posteriorly to form the dorsal aorta, contains only pure blood. This must have meant a great improvement in vigour of life—the supplying of the body with pure blood only, and the complete separation of pure and impure blood in the heart. It is not suggested, of course, that the primitive birds had a heart as well equipped as that of modern forms, for the heart has doubtless been subject to progressive improvement for ages. Our suggestion is that antecedent to flight there was an improvement in the circulatory system which made attempts in the direction of flight more probable.

§ 4. WARM-BLOODEDNESS

Another pre-condition of the bird's success was warm-bloodedness, that is, the power of regulating the temperature of the body so that an approximate constancy is sustained. Heat is produced in the oxidations or combustions that go on in the body, chiefly in connection with the muscles, and this heat, if not excessive, facilitates chemical reactions. If there is a very low temperature in the outer world, the body of the cold-blooded animal loses too much heat, and the vital reactions are slowed down. In the warm-blooded mammal in a very cold environment the loss of heat can be lessened by constricting the blood-vessels in the skin, or it can be counteracted by producing more heat internally. The same is probably true of birds, but they have not been much studied in this connection. When the warm-blooded animal is in a very warm place and has itself an internal rise of temperature, the danger of this may be counteracted

by a dilatation of the superficial blood-vessels, by increasing the evaporation of water in sweating and breathing, and to a slight extent, perhaps, by decreasing the internal production of heat, *e.g.* by keeping very quiet. As birds have no sweat glands, the regulation of a high internal temperature, consequent on intense metabolism, is effected to some extent by the evaporation of water from the internal surfaces of the lungs and air-sacs. This may be aided, perhaps, by a reduction of activities in very hot weather or in the hottest part of the day.

In any case, in a cold country and during a cold night, the adult bird is able to keep its normal body-temperature constant; and similarly in a warm country and during the heat of the day. This is effected by an intricate nervous mechanism which regulates production and loss of heat. And just as this regulatory arrangement is gradually established in the individual bird, so it must have been in the race. It is plain that as it was established it would make life an easier problem for the bird. It is also plain that the coat of non-conducting feathers would greatly assist the conservation of the internal heat in cold surroundings.

§ 5. FEATHERS

There is no doubt that the bird's solution of the problem of flight is bound up with the evolution of feathers, forming a sail that strikes the air. But on the evolution of feathers, which may have taken a million years, we have no light. We wish to suggest, however, that there may be an advantage in a flank attack, namely, in recognising the import of plausible pre-conditions of the power of flight. Other things equal, activity and a good circulation will tend to favour the development of integumentary structures, and birds are by hypothesis creatures of intense metabolism, fine vascular system, and great activity. There is also a marked abundance of blood-vessels in the bird's dermis.

No one knows how feathers evolved. All that is clear is that there is a general resemblance in the development of

reptilian scales and the development of birds' feathers. Both arise as flattened outgrowths of the epidermis which become cornified; both are imbedded in the dermis and fed by a basal core of dermis. But a reptile's scale is not moulted as a whole as a feather is, only the outer layer of the epidermis covering the scales; and, although birds usually show scales on their feet, there is not any transitional form between bird-scale and bird-feather. But we must return to this subject.

§ 6. ADAPTATIONS ACCESSORY TO FLIGHT

When flight had become an actuality, the achievement would be followed up by adaptation after adaptation within the body. The skeleton would become more lightly built; there would be fusion here and suppression there; the wing would be perfected by reduction of parts; the breastbone would get its keel; the tail would be reduced; the neck would be lengthened; the beak would become a hand; the balancing of the aerial boat would be adjusted; the useless muscles would dwindle and the useful ones would grow in strength; the feathers would be differentiated into pinions, contours, and the like. In short, there are many characteristic features of birds which must be interpreted as adaptations conspiring in the direction of improving flight. It is natural to think of these as being gradually added on after the problem of flight had been solved. They are accessories rather than pre-conditions.

Another peculiarity of birds, which may have been a pre-condition of flight or a subsequent accessory, concerns the respiration. The lungs are firmly fastened dorsally to the ribs and they are inexpandible. They are compressed by the pressure of the ribs in particular, and more generally by the springy basketwork formed by the thoracic vertebræ above, the breastbone below, and the ribs between. The active part of respiration is *breathing out* or expiration, whereas in mammals, as every one knows, the active part is *breathing in* or inspiration. Now it seems of radical

importance that in the flight of the bird the actual movements help respiration, abetting the expiration of air from the lungs. It cannot be a coincidence that in insects, which are the birds of the Invertebrate sub-kingdom, expiration is also the active part of the breathing process, and that the flying should help in this. A quickly running mammal is apt to get "out of breath"; a quickly flying bird is helped to breathe by the movements of locomotion.

To this must be added that the lungs, though relatively small, have a complicated internal structure with a large absorptive surface, and that their associated air-sacs allow of a "double tide" in respiration. When the lungs are compressed the vitiated air passes out by the wind-pipe, but unvitiated air comes in from the reservoirs or air-sacs. In the passive inspiratory process when the lungs regain their normal size, there is likewise a refilling of the air-reservoirs.

§ 7. MENTALITY OF BIRDS

One of the most marked differences between birds and reptiles is in the size of the brain in proportion to the size of the head and the body generally. The crocodile's brain is almost ridiculously small compared with the huge head; the bird's brain fills a relatively large cranial cavity, and there is a strong development of the cerebrum and the cerebellum. Can any light be thrown on this salient feature, which is consonant with the general improvement of the central nervous system as we ascend the Vertebrate series?

There are several reasons why variations in the direction of enlarged and complexified brain would pay particularly well in birds. The majority are small creatures, of delicate build, with little in the way of weapons or armour, and therefore more dependent than reptiles on their brains or wits. Moreover, the terrestrial life which amphibians practically began (among Vertebrates), which reptiles made more secure, has its own peculiar risks. The terrestrial animal is limited to one plane of locomotion, unless it becomes a burrower, or arboreal, or a flier. It is therefore

particularly important that the movements should be quick and precise. Furthermore, when birds became fliers, able suddenly to evade their enemies by rising into the air, they regained, as it were, the many-sided possibilities of locomotion that free-swimmers enjoy. And the brain is in great part an organ for the co-ordination of movements.

Perhaps, however, one may go deeper. There is no doubt that birds express one of the trends of organic evolution which may be described as the economising of reproduction. They have usually a sharply punctuated reproductive period and a small family. The flying habit has made it possible to deposit the eggs in safe places, and variations in the direction of reduced reproductivity must have been correlated from the first with variations in the direction of increased parental care. These are indissoluble except in very peculiar cases. The comparative safety secured for the eggs and young allowed of a long period of development before hatching, a possibly long sheltered period of infancy in the nest, and a possibly long nurture period in which the capacities of the young creatures are educated and new departures tested. All this surely favours the improvement of the brain and its correlated mentality.

With the alertness that is as characteristic of most birds as it is essential may be associated the fine development of the senses of sight and hearing.

Always returning to the heart of the matter, which is the power of flight by means of feathers, we can understand why flying creatures should have a sharply punctuated reproductive period. It is plainly advantageous for the female at least (and the males would have to follow) not to have a large ovary throughout the greater part of the year. As a matter of fact, the gonads sometimes dwindle almost out of sight. Now this punctuation of the reproductive period probably means greater intensity of the associated emotions between mates, and may be correlated with that heightening of feeling which overflows in song. Given considerable vocal powers, originating as sex-calls and elaborated into courtship ritual, there is an opening up of

PLATE II



[Photo by Rattar, Lerwick.]

KITTIWAKES (*Rissa tridactyla*) AND GUILLEMOT (*Uria troille*).

The Guillemot belongs to the Ringed or Bridled variety, with a marked white furrow behind the eye. The narrow shelves on the precipitous sea-cliffs are crowded with brooding birds.

wider uses of the voice in parental warning and instruction and in the sociable gossip of parrots. The expanding utilisation of the voice and the socialisation that it made possible, so familiar in the case of rooks, which have quite a vocabulary, would react on the evolution of the brain, would, at any rate, supply the sieve by which germinal variations in the direction of better brains would be approved of.

§ 8. NESTING

Accepting the hypothesis that birds evolved from a bipedal stock of terrestrial reptiles, we get a little light on the custom of nesting. Leaving the water was no doubt a step of progress, but it brought with it certain penalties. The terrestrial creature is confined to movement in one plane, the surface of the earth, and it cannot, like the fish or the frog, simply shed its eggs into the cradle of the water. And it must be remembered that the conquest of the land was associated with the establishment of *internal* fertilisation. Some reptiles transcend the first limitation referred to by becoming burrowers, like the limbless lizards and a few snakes; others by becoming arboreal, like chamæleons and the little dragons (*Draco volans*) the turtles and sea-snakes have returned to the sea. Similarly, as regards the disposal of the eggs, they may be buried deeply as in the Crocodile, they may be laid in a hole in a tree, or they may be incubated as in Pythons.

If, then, we think back to the incipient non-flying birds, without much in the way of armour or weapons, we can imagine the advantage of being able to take a running leap on to the branch of a tree and the advantage of having a nest in a position of relative safety. Later on, it need hardly be said, secondary advantages became manifest, *e.g.* making the nest such that the developing eggs were not liable to chill and that the nestlings were not liable to fall out. It should also be borne in mind that the nest may have had primitively a function to serve as a relatively safe retreat for pairing.

§ 9. MIGRATION

Finally it seems permissible to link on to the unified harmony of bird characters the very widely expressed custom of migrating. Given the power of flight, which means rapid escape from areas where food and drink have become scarce, and where other conditions, such as temperature, occasion discomfort, the possibility is opened up of circumventing the difficulties of the seasons. From the summer nesting quarters, when scarcity and cold set in, the migrants fly to easier winter quarters where they can rest and recuperate. From the winter quarters, when these become too warm for safe brooding and too dry for the bird's thirst, the migrants return to the country of their birth. The details do not concern us now, but it does not seem far-fetched to say that the migratory custom, which is now an organic impulse in a large proportion of birds, is congruent with the salient characteristics of the class.

The object of this introductory chapter is twofold: first, to suggest that many of the salient characteristics of birds are congruent or correlated; and second, to think back to the deep constitutional characteristics which may have been the pre-conditions of flight. These deep characters are intensity of metabolism, spare muscular habit of body, rapid bipedal progression, the supply of the body with arterial blood exclusively and that of fine quality, warm-bloodedness, the assisting of respiration by locomotion, and a well-developed brain. Given these features and others, it seems easier to understand how the evolution of feathers would make flight possible. And then would follow a score of secondary adaptations to flight.

CHAPTER II

EXTERNAL FEATURES BIOLOGICALLY CONSIDERED

§ 1. Shape and Pose. § 2. The Skin. § 3. Plumage of Birds.
§ 4. Moulting of Feathers. § 5. Coloration.

§ 1. SHAPE AND POSE

IT may be said that there are two main shapes among birds—*(a)* the Running Bird type, with considerable erectness, familiar in ostriches and also in some young birds like chicks, and *(b)* the Flying Bird type, where the body is more boat-like and the whole attitude less erect. When a Flying Bird or Carinate is adapted more to terrestrial than to aerial locomotion, the shape and pose have a superficial approximation to the Running Bird type, as is very well seen in a bird like the Bittern which has a somewhat flagging flight and often stands very erect like an overgrown chick. When, on the other hand, the Flying Bird is much given to swimming or to swimming and diving, the bulk of the body is very boat-like, the neck often rising at right angles. When a bird markedly adapted to aquatic life has its legs very far back, its pose on land may be very erect, and as the instep of the foot may then be flush with the ground instead of at right angles to it, as in most birds, the creature looks almost as if it were sitting on its tail. The instep may be on the ground; yet in the familiar case of the puffin, which looks as if it were resting on its tail, the bird is almost always standing on its toes in the orthodox way.

It is evident that the peculiarities of the plumage contribute not a little to what is characteristic in a bird's external appearance. A tern is marked by its long narrow wings and its forked tail, but this individuality is gone when the

bird is plucked. The graceful smooth lines so pleasing in most birds are in great part determined by the overlapping contour feathers of the body, and the naked creature is rather a sorry spectacle.

§ 2. THE SKIN

As if the skin exhausted itself in feather-making there is a striking paucity of skin-glands, for there is usually nothing but the preen-gland at the root of the tail, and even that is absent in ostrich, emeu, cassowary, and a few flying birds such as bustard, some parrots, and some pigeons. The fantail variety has none. The preen-gland is best developed in aquatic birds, where the secretion is believed by many to help in water-proofing. Whereas the mammal's fur is kept sleek, for the most part, automatically, by the secretion of the sebaceous glands at the roots of the hair, though licking the fur is familiar in the cat and some other cases, the feathers of birds are individually cleaned in the bird's bill, and the widespread belief is that this is aided by the oily secretion of the preen-gland. The bird reaches back with its mobile neck and is supposed to get drops of oil from the gland, which it proceeds to distribute over the feathers.

Mr. Pycraft points out (1910, p. 15) that many birds with a well-developed oil-gland could not possibly take up and spread so much as one drop of this precious fluid. Thus in the Scissor bill (*Rhyncops*) both jaws are compressed to form a single blade as flat as a paper-knife. Moreover, many birds without an oil-gland, *e.g.* bustards and ostriches, keep their feathers in as good condition as those birds which possess the organ. Mr. Pycraft suggests that the gland may be of use in producing a characteristic scent, serving for the recognition of kin. On the other hand, birds seem to be on the whole very deficient in the sense of smell.

The structure of the preen-gland has been very thoroughly studied by P. Paris (1913), who regards it as

closely allied to the odoriferous glands of some reptiles. It is a subcutaneous mass of glandular tubules surrounded by a capsule of connective tissue without smooth muscle-fibres. It is made up of two equal lobes, entirely or partly separate, united at the apex in a projecting nipple. Each of the lobes is autonomous, that is to say, each has its own supply of blood-vessels and nerves, and can secrete independently of the other. Each lobe has usually at least one efferent duct opening by the nipple, but in goat-sucker and hoopoe there is only a single duct for the whole gland. The excretory nipple, invested by the delicate skin, encloses the efferent canals of the lobes and the terminal portions of their enveloping capsules. Its extremity may be naked or furnished with plumules or exceptionally with pennæ, and there may be strands of smooth muscle-fibres.

Three types of preen-gland are distinguished by P. Paris (1906): (1) With the two lobes coalesced, a strong reservoir, a globular delicate nipple, without a terminal tuft of down, *e.g.* in sparrow, blackbird, and rook; (2) With the two lobes clearly defined, a strong reservoir, a long delicate nipple, and a feebly developed terminal tuft of down, *e.g.* woodpecker; (3) With distinct lobes, no reservoir, a short truncate nipple with thick muscular walls, and a strong terminal tuft of down, *e.g.* stork, heron, flamingo, and cormorant.

According to Paris, the importance of the preen-gland as supplying a lubricant or varnish to the feathers has been much exaggerated. Removal of the gland in starlings, wild duck, and some other birds was not followed by any change in the state of the plumage. Obstruction of the canals, *e.g.* in the fowl, seems to make no difference. The secretion is fatty, varied in colour, without excretory products, but with a characteristic odour. Paris did not find that the secretion was of use in increasing the impermeability of the feathers. It had no toxic action in the birds he studied, and neither its removal nor its hypertrophy had any effect on the health of the bird.

It may be suggested, however, that although the secretion

does not increase the impermeability of the feathers, it may increase the flow of salivary juice which is used in keeping the feathers clean.

The occurrence or non-occurrence of the preen-gland is rather difficult to interpret, for it may be absent in the near relatives of birds that have it well-developed. It is usually best developed in birds which frequent water, but while it is large in the white stork, it is small in herons. It is present in embryo *Ratitæ*, but seems to persist in the Kiwi only.

Scales.—Epidermic scales, sometimes small and granular, sometimes coalesced into large shields, usually cover the toes and the (tarso-metatarsal) region between the ankle and the toes. They are reminiscent of reptilian scales, but no one has found any connecting link between scale and feather. In some birds, like the grouse, sand-grouse, and owls, the feathers extend to the tips of the toes. This may be a primitive state, and Davies maintains that the scales on birds' feet are secondary transformations of feathers—a view requiring consideration.

Claws are specialised scales, and it is interesting to find that they are moulted in the grouse in the autumn, disclosing new sharp claws beneath the old ones which are discarded. Many birds have a claw on their thumb, and in rare cases, *e.g.* ostrich, there is a claw on the second digit as well. In the Hoatzin (*Opisthocomus*) the young bird makes considerable use of its thumb-claws in clambering on the branches. In old-fashioned birds, like albatross and petrel, the horny sheath or bill covering the bony beak, both above and below, is compound, and its component parts are equivalent to separate scales in reptiles. It is interesting to find in the puffin an annual moulting of the outermost parts of the bill-scales. In this and in the moulting of the claws of the grouse there is an echo of reptilian moulting, where there is a periodic shedding of the outermost layer of epidermis which covers the scales. The moulting of feathers, where the whole epidermic structure, comparable to a scale, is moulted, is a unique

phenomenon—quite different from reptilian moulting and more like the shedding of hair.

As long as the ancestral birds were still provided with teeth, the covering of the jaws with horny scales would be of minor importance. But with the loss of teeth the condition of affairs was changed. Thus, as Lönnberg (1904) maintains, the reptilian *rostral* scale became greatly enlarged on the upper half of the bill and the reptilian *mental* on the lower jaw. This illustrates a frequent *method of evolution*—making a new thing, in this case the sharp-edged horny bill, out of a very old thing, in this case the scales of the reptile's jaws.

The epidermis as a whole is relatively thin as compared with that of mammals. It has no sweat-glands and there is usually only the preen-gland. In a few cases there are some gland-cells beside the ear-opening. There are abundant tactile nerve-endings (Pacinian corpuscles) in the skin, and these are often specially developed in a swollen patch or cere at the base of the bill. In birds like woodcock and snipe that probe for their food in soft soil or in mud, there are nerve-endings in the delicate skin continued to the tip of the bill. In ducks and the like there are many nerve-endings along the inner margin of the bill. Here it may be noted that the New Zealand Kiwi or Apteryx is the only bird with the nostrils at the tip of the bill; in other cases they are at the base of the bill, except that in albatrosses, petrels, and their relatives the openings are carried well forward dorsally in a horny tube. In some cases, such as the gannet, the openings of the nostrils are closed up altogether.

A few other external features must be noticed. There is no ear-trumpet or pinna, though there is a little flap in owls, and the absence of this apparatus for collecting the sound waves may be connected with the mobility of the head. The reduction of the pinna in man as compared with its large size in the donkey may be in part referred to the same correlation, for it is easy for man by adjusting his head to catch and localise faint sounds. Every day in the

street we see horses turning round the pinna of their ear on occasions when we should adjust our whole head.

The development of skin-outgrowths to form combs and wattles and similar structures will be discussed in connection with sex, for they are usually most marked in the male bird.

One of the most peculiar external characters, which has been much discussed without great result, is the serrated or pectinated claw of the nightjar. It also occurs in the bittern, gannet, heron, and courser. Perhaps it has to do with some sort of preening. Like various peculiarities in beaks, as in the Skimmer, the pectination is not found in the nestling, but develops later. This is decidedly against one of the theories, that the pectination is a vestigial structure which has lost the function it had in some bygone ancestor, and is no longer of any importance.

§ 3. PLUMAGE OF BIRDS

Uniqueness and Specificity of Feathers.—A bird is known by its feathers. This familiar statement expresses two facts—(a) that feathers are strictly confined to birds, and (b) that different types of birds have different types of plumage. (a) Although a feather is like a scale in being an epidermic structure and in its simplest forms may be thought of as the frayed-out base of a scale, there is no connecting link between scale and feather, and, as we have seen, the evolution of feathers is quite obscure. (b) It has been shown by Chandler (1916) and others that relationships between birds, as indicated by skeletal and other parts, are often corroborated by characteristics in the structure and distribution of the feathers. The important points are in the aftershaft, the barbs, the distal barbules of the pinions, and the degree and manner of simplification seen in the barbules of the body-feathers. Since the number of minute structural units composing a feather is large there is more opportunity, as it were, for the expression of specificity than there is in the scale of a fish. Moreover,

the minute structural differences between feathers are seldom adaptive, which increases their taxonomic value. As many a bird can be identified from a single feather we need say no more in regard to specificity.

Structure of a Typical Feather.

—An ordinary contour feather or penna shows the following parts : (1) the cylindrical hollow barrel or calamus, the base of which is embedded in a moat or follicle of the skin ; (2) the main shaft or rhachis, filled with white pith, somewhat quadrangular in cross-section, but convex externally and with a longitudinal furrow along its internal surface next the skin ; (3) the vane, consisting of a bilateral web, which in the case of the pinions serves to strike the air, and is built up of barbs, barbules, and barbicels ; and (4), it may be, an aftershaft or hyporhachis, which arises to the inner side at the little pit marking the junction of calamus and rhachis, and consists of a tuft of barbs often with barbules. The basal part of the vane is often downy. The term " quill " should include calamus and rhachis ; the minute opening through which the pulp of the dermis enters the base of the calamus in the growing feather is the inferior umbilicus ; the pit at the junction of the calamus and rhachis is called the superior umbilicus ; the transparent partitions across the interior of

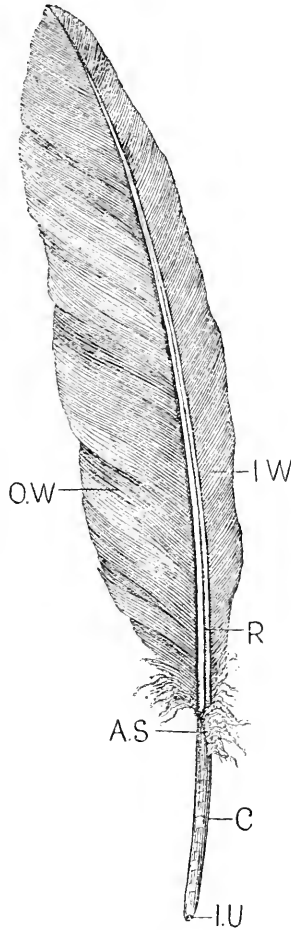


FIG. 1.—A typical feather. R., rhachis ; I.W., inner web of vane ; O.W., outer web of vane ; A.S., aftershaft ; C., calamus or quill ; I.U., inferior umbilicus where pulp enters.

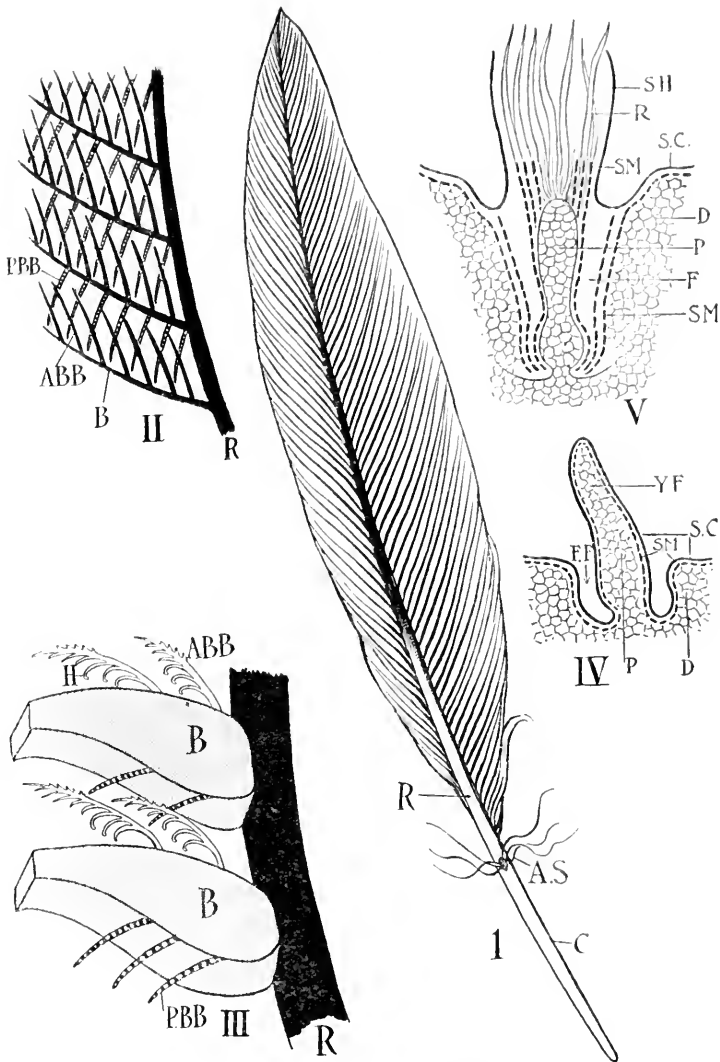


FIG. 2.—Structure and Development of the Feather (diagrammatic).

I. An ordinary pinion; C., calamus or quill; A.S., aftershaft; R., rhachis.

II. An enlarged part of the vane; R., rhachis; B., barb; A.B.B., an anterior barbule; P.B.B., a posterior barbule.

III. Two barbs (B) enlarged; A.B.B., an anterior barbule; H., hooklets; P.B.B., a posterior barbule.

IV. An incipient stage in the development of a feather; Y.F., young feather; P., the internal pulp or

dermis; F.F., the feather follicle; D., the dermis; S.C., stratum corneum of the epidermis, which forms a sheath; S.M., stratum malpighii which forms the feather.

V. A later stage showing a layer of the stratum malpighii becoming cornified into barbs (R), the sheath (S.H.), the other letters as before. The stratum malpighii is shown as interrupted lines. Other letters as in IV.

the calamus, marking the retreat of the pulp, may be called the "caps"; the barbs are also known as rami, the barbules as radii. The barbicels or cilia are outgrowths of the barbules, and some bear microscopic hooklets or hamuli which are linked to the barbule next in front.

"Under a high magnification of the microscope these barbules will be found to consist of two very distinct kinds, ranged one on either side of the barb. Those on the side of the barb pointing to the tip of the feather have the appearance—when examined separately—of flattened plates, cut up, from the middle outwards, into a number of long, hooked filaments, while those of the opposite side of the barb take the shape of long scrolls, whereof the upper edge is the more deeply curled. When *in situ* the two series are so arranged that the hooklets are thrust down between the scrolls so that their curled edges are caught thereby" (Pycraft, 1910, p. 7).

Professor Newton notes that on one of the primary feathers of a crane he found 650 barbs on the inner web, that each of these barbs bore about 600 pairs of barbules, making 780,000 barbules for the inner web alone, and therefore far over a million for the whole feather. And then there are the barbicels!

Kinds of Feathers.—There are three chief kinds of feathers—(a) the ordinary contour feathers or pennæ, whether covering the body as a whole or specialised as pinions (remiges) and tail-feathers (rectrices); (b) the down feathers or plumules, whether confined to nestlings or persisting throughout life; and (c) the hair-like filoplumes, which are hardly seen until the others have been plucked off.

Some of the peculiar feathers, such as bristles about the gape, eyelashes, and ornamental plumes, may be derived from contour feathers. Others, like powder-down and oil-gland feathers, may be referred to the plumule type. It need hardly be said that filoplumes, bristles, eyelashes, and the like, show no real approach to mammalian hairs except in shape.

In powder-downs the calamus forms no rachis, but splits into barbs and barbules which disintegrate into apparently greasy powder. They occur in many birds, sometimes in patches as in herons and bitterns, sometimes in scattered tracts and tufts as in parrots, the roller, and the immature Lämmergeier (*Gypæetus*). In the bittern the tufted calamus is about half an inch long; in the more-pork

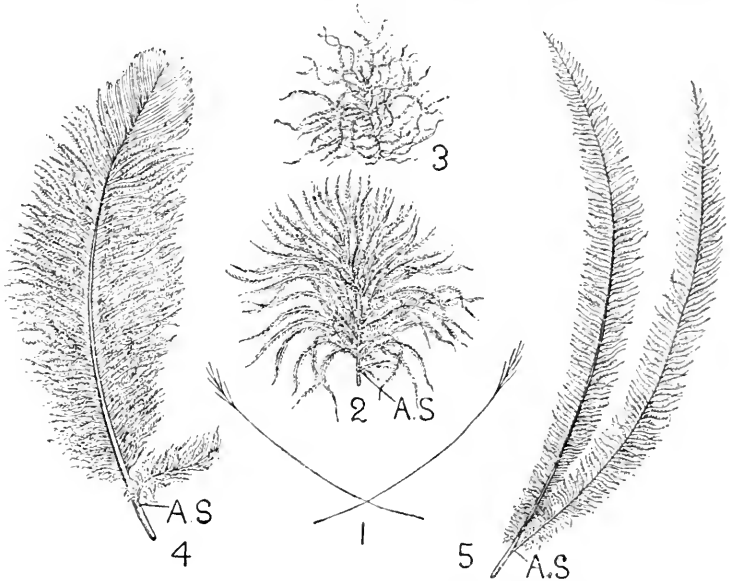


FIG. 3.—Different kinds of feathers: 1, filoplume; 2, a permanent down-feather, with aftershaft (A.S.); 3, a nestling down-feather; 4, a feather with free barbs; 5, an emu's feather with very long aftershaft (A.S.).

(*Podargus*) the maximum of two inches is reached; but in most cases the powder-downs are very small. Their use is obscure. It has been suggested that they help to keep the plumage clean and in good condition—a sort of feather-powder.

Powder-down feathers are peculiarly specialised down-feathers, but they do not seem to be the same in every case. The powder is formed by the degeneration of the cellular sheath covering the barbs, and Schaub has shown (1907)

that there is no fat present, as is sometimes alleged. The greasy feeling is due to the mechanical nature of very flexible minute platelets of horn.

What are called tactile feathers or vibrissæ occur at the root of the bill and round the eyes, and are best developed in nocturnal birds. According to Küster (1905), they owe their tactility to touch-corpuscles at their base; the nerve-fibres that enter the papilla have only a vaso-motor significance.

Uses of Feathers.—(1) There can be little doubt that the primary use of feathers is to form a relatively non-conducting covering which tends to retain the animal heat. This value may be increased in very cold environment by the quality of whiteness, as in ptarmigan and snowy owl.

(2) Secondly the feathers made flight possible. As adaptive to this may be noted the light elastic build of these horny structures, the close almost air-tight linkage effected by the barbules and the hooklets of the pinions, and the relatively great length often attained, far exceeding that of the bones which bear them.

(3) The feathers may help to render the bird inconspicuous by their close resemblance to habitual surroundings. Thus the brooding woodcock among the fallen leaves and withered herbage has what may be called a garment of invisibility, and the white winter plumage of the ptarmigan very effectively hides the bird among the snow.

(4) The feathers are often auxiliary to the appeals made in courtship activities. They may be of such a structure that they enhance the brilliance of the bird as it moves about; they may form elongated decorations as in the streamers of some Birds of Paradise; they may be erected in excitement, as is familiarly seen in pigeons; they may be used to produce sounds which arrest attention, as in the "drumming" snipe.

(5) In a great many cases, reaching a climax in eider-duck and long-tailed-tit, feathers are used in the formation of the nest, and not only conserve the heat around the imperfectly warm-blooded nestlings, but make the brooding

parent more comfortable. The eider-duck in leaving her nest for a meal draws the quilt of down over the eggs. MacGillivray counted 2379 feathers in the "feather-poke" nest of the long-tailed-tit. They belong to other birds.

(6) A number of peculiar uses may be grouped together. We have already mentioned the belief of some ornithologists, that the peculiar powder produced by the disintegration of the powder downs in herons, bitterns, parrots, and other birds is useful in keeping the plumage in good order and checking the multiplication of ectoparasites. It is seen as a bloom on the beak and face of the African parrot and on the beak and face of cockatoos.

Other feathers form the eyelashes and others project near the base of the beak, both probably akin to filoplumes.

It is probable that conspicuous white patches, as on the wheatear's rump, may help to distract the eye of the bird of prey from the more vulnerable head. It may also be that conspicuous markings help in the recognition of kin by kin.

Succession of Plumages.—Many a young bird, like the pigeon squab, is practically naked when newly hatched; its skin shows numerous feather tracts or pteryllæ—rows of pits or follicles—which form a characteristic pattern. The succession of different sets of feathers is not altogether clear; we shall begin with an outline of the usual version of the story.

There is in most cases a preliminary nestling suit of down-like feathers, which are technically called "neossoptiles" (Greek, neossos, a chick), in contrast to the subsequent adult feathers or "teleoptiles" (Greek, teleos, mature), whether these be contour feathers or downs. In typical cases some of the nestling down feathers (called prepennæ) are immediately succeeded by contour feathers of the adult type, while others (called preplumulæ) are succeeded by adult down feathers. In some cases, *e.g.* nestling Owls, only prepennæ are developed; in other cases, *e.g.* nestling Cormorants, there are only preplumulæ. In a few cases the bird has no feathers before the teleoptiles.

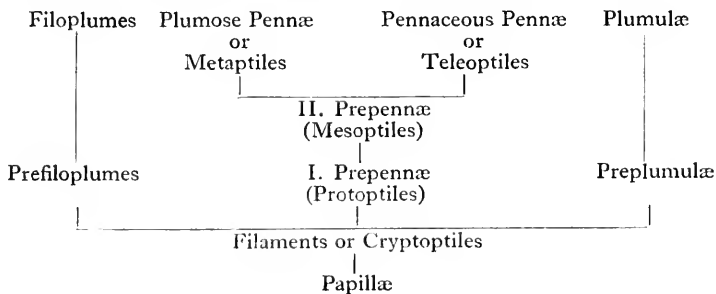
The down-like nestling feathers or neossoptiles are

almost always primitive, less specialised than the down feathers of the adult if it has any. Thus in most cases the calamus is very short, the rhachis is absent or ill-defined, the barbs are long and slender, the barbules are numerous, the barbicels are absent. There is no aftershaft except in the Emeu. Penguins are remarkable, since the minute structure of the adult down feathers is the same as that of the young, which resembles the nestling down of ducks, rails, and cormorants. This hints at primitiveness in penguins. In ostriches the nestling feathers show their highest development; thus the calamus is well-formed and the barbs of the back feathers are terminally expanded and flattened, giving the chick a coarse bristly appearance.

Furthermore, it is usual to distinguish two sets or generations of prepennæ—the first set called protoptiles and the second set called mesoptiles. The penguins show the two sets very clearly, but in most birds there is only one nestling coat, and it is a difficult question to decide whether this represents the first or the second set. The protoptiles or the mesoptiles may be vestigial or even suppressed.

The adult pennæ may be divided into plumose and pennaceous types. The plumose pennæ, not to be confused with adult down feathers, have no hooklets or hamuli on their barbules; the pennaceous pennæ have some of their barbules equipped with hooklets binding the barbs into a coherent web.

The following scheme, which we have ventured to invert, is suggested by Professor Cossar Ewart (1921):—



Professor Cossar Ewart's Recent Work.—Some of the observations made on the mallard and other birds by Professor Cossar Ewart show that we are far from security or clearness in regard to the succession of plumages, and we propose to sum up his more important conclusions. These have, of course, to meet the criticism of other investigators.

The coat worn by newly hatched ducks and geese corresponds to the first or protoptile nestling coat of penguins. The second set (mesoptiles) is disappearing, though still represented on the wing.

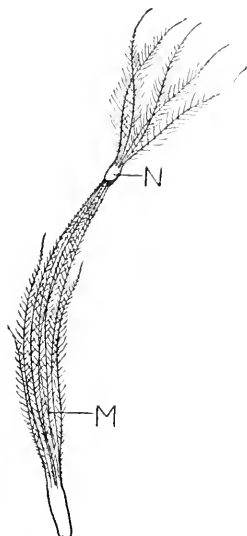


FIG. 4.—A mesoptile (M) pushing out its predecessor, a protoptile (N).

The wing-quill protoptiles are complete feathers, with a calamus, a shaft, and an aftershaft. Though small, they are complete; with short stiff, as well as long, slender barbs; with well-developed and in some cases hook-like cilia; and with a well-developed aftershaft, the barbules of which bear cilia. Thus there is nothing degenerate about these protoptiles.

But the mallard has mesoptiles (second set) well-developed as well as protoptiles. They occur as wing-coverts and wing-quills. Both sets may be seen in the mallard duckling at the end of the sixth week, but all are usually lost before the middle of the eighth week.

The nestling tail of the mallard duckling, of importance in early diving, consists at first of eighteen protoptiles. During the second week these are pushed from the skin by the tail-quills, or by vestigial mesoptiles. For the rest of their diving period (six weeks) the mallard ducklings use teleoptile tail-quills. There are vestiges of two tail-quill mesoptiles, so that even in the tail there is distinct evidence of two generations of neossoptiles.

The prepennæ of the body generally (head, neck, trunk, and hind limbs) are mostly protoptiles, sometimes so poorly developed that they are like preplumulæ. Some of the trunk pennæ are preceded by mesoptiles. The general inference is that the second nestling coat of prepennæ is in process of suppression.

The preplumules of the mallard are in most regions hidden by a relatively dense coat of protoptiles. The plumules usually consist of a calamus, a shaft, and an aftershaft; both shaft and aftershaft bear long slender barbules marked by characteristic pyramidal swellings.

A study of the structure and development of filoplumes points to the conclusion that filoplumes are degenerate pennæ, nearer to protoptiles than to preplumulæ; and filopenna would be a better name than filoplume.

The development of the aftershaft indicates that it is a primary not a secondary feature. It grows from apex to base, and is completed before the calamus is formed. Moreover, the tip of the aftershaft is connected with the calamus about to be shed. If this be the case, then a complete true feather (penna), like a down feather (plumula), consists of two shafts or blades. It is the reduction of the aftershaft that is secondary, and Professor Ewart's investigations show that the presence of a strong aftershaft is more frequent than is usually supposed.

Professor Ewart is strongly opposed to the view that feathers evolved from scales. "It is inconceivable that the small protoptile forerunners of the wing-quills of Ducks were evolved from enlarged scales, which as they increased in length became fimbriated. The more the history of feathers is studied the more untenable becomes the belief in their origin from scales." The embryological evidence only shows that the feather arises, like the scale, from a papilla of epidermis fed by a core of dermis. There are no hints of transitions between feathers and scales.

Of the evolution of plumage Professor Ewart gives a very interesting provisional sketch. "A study of the development of birds suggests: (1) that their coat, to start

with, consisted of various kinds of simple filaments ; (2) that in course of time the hollow epidermic cone in each filament, in some incomprehensible way, was converted into a protoptile or preplumula ; (3) that the protoptiles in some cases soon acquired the chief characteristics of true feathers ; (4) that for a time progress was arrested in order to provide birds (or most of them) with a fur-like (mesoptile) coat, by way of giving them a chance of surviving during the cold phases of an Ice Age ; (5) that as the climate improved, the mesoptile coat was in many cases superseded by a coat of true feathers ; and (6) that by the specialisation of feathers along the posterior margin of the hands and fore-arms and the sides of the tail, birds of the Archæopteryx type were eventually evolved capable of flight, or at least of gliding easily from tree to tree."

Development of a Feather.—The early development of a feather is in a general way like that of a scale. A papilla projects on the delicate skin of the embryo (about the 6th day in the chick) ; this papilla has a core of dermis (mesodermic), which feeds the growing feather, and a covering of several layers of epidermis, an unimportant delicate epitrichium, a stratum corneum (forming a lining to the feather follicle) and the inner stratum Malpighii (forming the final feather and its transitory sheath). The papilla becomes a backward directed cone and sinks into a moat or feather-follicle which is largely due to the ingrowing of the Malpighian layer (Fig. 2, IV).

In the centre of the young papilla there is the nutritive pulp, around this a mantle of Malpighian cells, outside this the inturned stratum corneum, and outside this the dermis or under-skin into which the follicle has grown down.

But the Malpighian mantle differentiates into three layers—(1) the innermost delicate transparent sheath of the pulp, afterwards seen as the "caps" in the quill ; (2) the longitudinal rows of cornified cells which become the barbs and coalesce in a cylindrical tube or calamus at the base ; and (3) an external sheath which afterwards splits and peels off, liberating the barbs (Fig. 2, V).

The most important general fact is that the feather is altogether the result of a cornification of some of the cells of the Malpighian layer, and that the dermic pulp is purely nutritive. Like a reptilian scale, or a bird's scale, a feather is entirely an epidermic product.

The pulp and Malpighian mantle that formed a nestling down feather (Neossoptile) will go on to form a feather of the full-grown type. Professor Newton writes: "The short calamus of a Neossoptile is not closed at its base, but is again split into a number of columns of cells, which though not yet horny are the tips of the rami of its successor. As a rule the whole follicle sinks deeper into the skin, and thus comes to lie in a sort of pocket, which, occasionally reaching the periosteum of underlying bones, produces on the ulna the well-known roughnesses that correspond with the number of cubital quills."

A papilla that is going to become a quill feather shows two specially thick columns of cells on its dorsal and ventral surface. The former become the shaft or rhachis, the others the aftershaft or hyporhachis. "In fact," to quote again from Newton's Dictionary, "the rhachis is only a vast elongation and thickening of more than the dorsal half of the growing calamus which during its rapid increase carries with it most of the rami (barbs), while only those nearest the ventral median line of the quill remain in their original position, unless an hyporhachis be developed as a ventral elongation of the calamus."

A second generation of feathers is formed from the persisting follicles. A residue of pulp and Malpighian mantle is called into activity by the physiological conditions of a moult. The old feather is pushed out and another takes its place, and so on time after time, for the follicle has unlimited regenerative capacity. This has a further adaptive value since it may be awakened by the accidental loss of a feather. Professor Newton notes at the conclusion of his article on Feathers, that the 10-feet tail feathers of some Japanese cocks are evoked in some unknown way by checking the moult and yet stimulating the growth.

New Feathers.—Except in the case of the first feathers after the down, a new feather arises indirectly rather than directly from its predecessor. According to Frieda Bornstein (1911), a new germ arises, while the old feather is still growing, at one side of the base of the feather follicle. The new feather-germ forms a process which grows into the deeper layers of the cutis, and from this process the new papilla is formed. The old papilla atrophies after the old feather falls off.

Studies of feather replacement in fowls by Raymond Pearl and Alice M. Boring (1914) brought out the following points: (1) In the general body plumage a feather is not usually regenerated more than three times. Wing primaries have the maximum regenerative capacity. (2) If a feather follicle has been brought into a quiescent state by the successive removal of feathers and has remained absolutely inactive for a long period, *e.g.* six months, before the natural autumn moult, it nevertheless forms in connection with the moult a new feather, in the same manner as does any other follicle in the body. The process of moulting re-activates the follicle. (3) The precise pattern of the feather is usually reproduced each time with extreme fidelity of detail. But if the feather is removed from the follicle as soon as it is fully formed, thus forcing continuous regenerative activity, the patterns tend gradually to break up. It may be that the hereditary factor material in the feather follicle becomes exhausted if repeatedly called upon without due intervals. (4) The secondary sexual feathers of the male only appear as adult plumage. The follicles that produce them previously produced, as juvenile plumage, ordinary undifferentiated feathers. But if the juvenile feather be removed apart from the normal moult, the next feather will be a secondary sexual feather, and after that all the regenerations will be of the secondary sexual type.

The embryological evidence seems to suggest that a feather is something superadded to the scale-primordium—an extra-differentiation. Joseph Schleidt (1913) notes that the primordia of the scales on the chick's feet are very

like the primordia of Reptilian scales, and there seems to be no difficulty here. On the body of the grass-snake and of the chick, and on the feet of the chick, there are very similar structures, passing without definite limits into one another, forming a sort of rippling and due to proliferation of both dermis and epidermis. When feathers are going to develop there is on the second day a proliferation of epidermis at the apex and steep side of the papillæ, and the feather primordia becomes well-defined as if the rippling was smoothed out. The foot of the chick and the fore limb of the blackbird show embryonic down feathers on scales, and at a very early stage these down primordia are seen arising as special differentiations on the scale primordia. These facts seem on the whole to point to the conclusion that a scale does not correspond to more than the base of a feather.

The very opposite view is suggested by Bornstein (1911) who studied the foot of the capercaillie, where feathers and scales occur in close association. The conclusion he arrived at is that a feather corresponds not to an entire scale, but only to part of a scale, the rest being suppressed.

There is a geometrical precision about the disposition of the feathers, which is interpreted by S. Schaub (1907) in correlation with strains on the skin. He also points out that while there may have been a primitive diffuseness of distribution from which the geometrically orderly arrangements have evolved, a secondary diffuseness may arise in the definite plumage.

§ 4. MOULTING OF FEATHERS

The advantage of moulting, which is normally annual, is obvious, for it means a replacement of worn feathers. But it is not clear to what precise stimulus the activation of the follicle is due. Moulting usually takes place after the fatigue of the breeding season and before the autumnal migration, but in swallows, diurnal birds of prey, and some

other cases, it occurs in mid-winter. In reptiles what is moulted is the outermost dead layer of epidermis covering the scales, but in birds it is the whole feather. Thus the moulting of feathers is nearer the casting of hair in mammals.

The moulting is usually spread over a considerable period, but sometimes it is so rapid that the bird is left very naked. Moulting geese, ducks, and rails lose all their quills at once, and are for a time unable to fly.

The condition of things in penguins is very remarkable. It has been shown by Mr. W. P. Pycraft (1907) that penguins develop two successive down-plumages before assuming the normal definitive feathers. Another remarkable fact is that, in the penguin's moulting the feathers are not cast a few at a time, but in patches. Over large areas the feathers lose all direct attachment to the body, and stand out at right angles or thereabouts. It may be noted that penguins are antique birds, and that the distribution of the feathers (the pterylosis) is more primitive than that of other Carinatae. For although the penguins are flightless their affinities are with the flying birds.

Many birds moult, more or less completely, more than once a year; thus the garden warbler moults twice. There is often a partial or complete spring moult, after which the male birds put on special decorations for the courtship season, as may be illustrated by ruff and golden plover. The ptarmigan changes its plumage three times in the year; after the breeding season the plumage is predominantly grey; in the winter it is almost completely white; in spring the mottled brown wedding robes are put on. Mr. Pycraft suggests that there may have been to begin with three or more moults in the year, and that the number was reduced as the feathers were perfected. The reduction in number would imply a very advantageous physiological economy.

The suggestion readily arises that the "eclipse" plumage of a bird like the mallard may be correlated with some seasonal change in the testes. But this is not exactly confirmed by the observations of C. G. Seligmann and S. G. Shattock (1914), who have looked into the matter.

The testes of the mallard are active only during the winter months and in early spring, and inactive in summer, but there is no precise coincidence between the changes in the testes and those in the plumage. Yet the normal passage of the mallard from the full winter (breeding) plumage to its dusky summer (eclipse) plumage is delayed if castration is effected during the months whilst the gonads are assuming or have attained activity. The delay has its analogue in the well-established fact that if a colt is castrated when shedding its winter coat, the shedding is for a time arrested and thereafter proceeds very slowly. Further inquiry may show that the change of plumage is in some measure dependent on a testicular hormone; it has to be borne in mind that a small fragment of testes left during the operation may regenerate the entire organ. But the general vigour of the body is probably another factor.

One of the special cases of plumage change is what Charles Waterton called the "eclipse" of males among ducks. "The male, as soon as his expectations of a family are realised, that is to say, in June, doffs his coat of many colours and puts on a livery very closely resembling that of his spouse, and so closely that it takes an expert to distinguish the sexes at this time" (Pycraft, 1910, p. 277). This "eclipse" used to be regarded as an *interpolated* plumage giving the male a protective inconspicuousness, particularly important since the moulting duck is unable to fly, but it has been shown that the "eclipse" plumage corresponds to the "winter" or post-nuptial plumage of such birds as the plovers. An evolution is in progress among the ducks towards bright plumage, and the eclipse of the drake is a somewhat premature setting in of an evanescent dull phase. It lasts for a short time and gives safety; it is then succeeded by the brightly coloured plumage. As is usual in such cases, the facts are somewhat intricate, and it is difficult to avoid a false simplicity; but the biological gist of the matter is that we are face to face with a *temporal* variation, a shortening down of one part of the seasonal cycle and a lengthening out of another part.

Perhaps the most important experiments on moulting that have yet been made are those of C. W. Beebe (1914) on males of the Scarlet Tanager (*Piranga erythromelas*) and the Bobolink (*Dolichonyx oryzivorus*), in both of which a brilliant summer plumage alternates with a totally different winter garb. The factor investigated was the condition of fatness or thinness of the bird's body.

Tame tanagers and bobolinks which had not bred but were still at the height of vocal and physical condition were placed at midsummer in small cages in a quiet room. The light was gradually cut down and the food supply was slightly increased. The birds became quiet and inactive; they rapidly put on fat and increased in weight. The autumn moulting time passed without a single feather being shed. Midwinter found the birds in their summer dress, and it was noted that if one was temporarily brought into a stronger light and had meal-worms added to its diet, the song was fully resumed for a limited period. A sudden alteration in temperature, up or down, reduced the weight, and one of the tanagers, rapidly reduced, underwent a belated moult into the green winter plumage.

"Early in the following spring individual tanagers and bobolinks [from among those experimented on] were gradually brought under normal conditions and into their seasonal activities, with quick result." The spring moult took place, and the birds went directly from one nuptial plumage to another. "The old scarlet and black feathers fell from the tanagers, and were replaced by others of the same colour; and from buff, cream, and black, the bobolinks moulted into buff, cream, and black!" In every case the intervening winter plumage had been entirely suppressed. It may be noted that the green winter plumage of the male Scarlet Tanager is the permanent dress of the young of both sexes and of the adult female. It is presumably the ancestral garb.

Mr. Beebe's conclusion was that the condition of the birds as regards fatness or thinness determines whether they shall moult or not. The seasonal "pigmental changes

in the blood" go on as usual, but they are not expressed externally when there are no new feathers to be coloured. In the single tanager which was induced, by a sudden temperature change, to moult in winter, the green winter plumage appeared. In the others, which did not moult till spring, scarlet feathers succeeded scarlet feathers without the green potentiality ever finding expression. "We have thus proof that the outward manifestation of the sequences of plumage in these birds is not in any way predestined through inheritance bringing about an unchangeable succession, in the case of the tanager, of scarlet-green, scarlet-green, year after year."

This is a particular and striking case of the general biological theorem that every process of development—for the moulting is a continuance of development—has an intrinsic constitutional factor and an external environmental factor. In the case of Beebe's birds, the modified food and temperature brought about a bodily condition very different from the thinness and fatigue usually associated with the stress and cares of the breeding season. This was step one. The unusual vigour gave a new lease of life to the feather or obviated the onset of the moult. This was step two. The deferring of the moult made it impossible for the deeper pigmental change in the blood to find external expression. This was step three. What occurs normally is a harmonised correlation of internal constitutional rhythms and external seasonal periodicities.

§ 5. COLORATION

Birds and Insects are probably the animals of intensest life, and they are the most brilliantly coloured. There is some evidence of a physiological correlation here, that bright colours have something to do with rapidity of metabolism, that pigments may be sometimes the by-products or waste-products of intense living.

It is well known that animal coloration may be produced in three ways—(a) by pigments, (b) by physical structure,

or (c) by a combination of these. A high-coloured, ruddy countenance is due to the pigment hæmoglobin in the red blood-corpuscles. The blood in the capillaries of the dermis shines through the epidermis, and the skin is red, as in a cock's comb or a turkey's wattles. The red colour of a boiled lobster is likewise pigmentary. But the rainbow-like colours seen on many a shell, when the mother-of-pearl layer is exposed or when the inside of the shell is seen, are due to the physical structure, to the thin lamellæ of lime. When the shell is pounded small, there is only white powder, no pigment. A familiar characteristic of this sort of coloration is that the colours change as the object is moved about. The colours are "interference-colours," and entirely due to the splitting up of the rays of white light. The rainbow in a soap-bubble as well as in the sky is altogether apart from pigmentation, as every one knows. But, thirdly, some of the finest effects are due to a combination of pigmentary coloration and physical coloration, as we see on a peacock's tail or on a butterfly's wing. There is a sculpturing of the surface of the bird's feather or of the scales on a butterfly's wing which enhances the value of the pigment or pigments also present.

The iridescent colours on feathers have been referred to two causes, and it may be that the two interpretations hold for different cases. According to Gadow and others, the colours are due to dispersion phenomena caused by prisms or fine lines. According to Mandoul (1902), the colours are due to interference phenomena caused by delicate lamellæ in the superficial region of the feather.

According to Michelson and Walter, the iridescence is due to selective reflection from an intensely opaque material, and, in a few cases, to diffraction from a finely striated surface. According to Mallock (1911), interference of some sort is in most cases the active cause of the iridescence; although, in others, the possibility of selective reflection is not excluded. The question turns on the size of the "grain" of the colour-producing structure. Is it comparable with the wave-length of light or is it of molecular

dimensions? If the colours are due to interference, the first supposition must be true; but if selective reflection is the agent, a comparatively small group of molecules may cause selective reflection. Mallock found that the colour disappeared from feathers, butterfly scales, beetles, and flies when these were subjected to compression, and was thus led to the conclusion that interference of one kind or another is the true cause of natural iridescent colours.

The pigments of birds are mainly deposited in the feathers, but they also occur on the bare skin, on internal parts such as the roof of the mouth, in the fat of the body, in the yolk of the egg, and so on. Those on egg-shells will be discussed separately. Most of the pigments of birds, apart from egg-shells, fall into two groups—the lipochromes and the melanins. See Krukenberg, Newbigin (1898), Gadow (1893).

(1) The lipochromes or fatty pigments usually occur in solution in fats, but they are common in feathers and bill, as well as in fat and yolk. A very good example is zoonerythrin (animal red), seen in the "rose" around the eyes of Grouse, and in the red feathers of the Flamingo, the Scarlet Ibis, some Cockatoos, the Cardinal Bird, and others. It is of wide occurrence among animals and is familiar in the higher Crustaceans, such as lobster and crab, shrimp and prawn. It occurs along with fat or oil, and is soluble in alcohol, ether, and chloroform.

Related to zoonerythrin is zooxanthin, a yellow pigment, occurring in fat or oil diffused in many feathers. The bright yellow feet and bills of ducks and related birds and of some birds of prey probably owe their colour to zooxanthin.

(2) The second great group of pigments is that of the melanins, which produce most of the dark colours of birds. The pigment occurs in the form of small particles, not soluble in alcohol or ether. It is probable that the group of melanins is rather heterogeneous, but they have not been much studied either chemically or physiologically. In

some cases there is some indication of origin from the hæmoglobin of the blood.

Strong has shown (1917) that the dark pigment or melanin of birds' feathers has an epidermic origin in fowls at least, and appears in epidermic parts of the feather-germ. Some melanophore-cells also occur in the dermal pulp at the lower end of the feather-germ, but these do not pass into the feather.

(3) The hæmoglobin of the blood is a protein pigment, containing iron. It occurs in all Vertebrates and in many Invertebrates, and is of fundamental importance because of its power of capturing oxygen from the atmosphere (in the bird's lungs) and carrying it to the tissues. It is a good example of a protein that can be readily got in crystalline form (blood-crystals), though it never occurs in that form in the living animal. Of great interest, as illustrating the individuality of each species, is the fact that the form of the blood crystals in nearly related mammals is different. It is probably the same with birds, for specificity is a general fact in regard to different kinds of living creatures.

Hæmoglobin gives origin to other pigments, such as bilirubin—the reddish pigment of the bile, which in turn is the mother-substance of others; such as the green biliverdin of the bile and the urobilin of the urine.

(4) A number of peculiar pigments may be grouped together. Very remarkable is turacin discovered by Church (1869 and 1893) in the red feathers of the African family of Plantain-Eaters (Musophagidæ). It also occurs, according to Krukenberg, in one of the Cuckoos, *Dasylophus superciliosus*. It contains 5-8 per cent. of copper, as is indicated by the green flame shown by the feathers when burnt. The pigment is so soluble that it is washed out by the rain, and when birds take a bath they colour the water red. What is lost is of course replaced. Also in Plantain-Eaters is turacoverdin, the only green pigment in birds, containing iron but no copper. There are, of course, many instances of green colour, but there is only this single occurrence of green pigment; and similarly it may be noted that while

many feathers are blue or white there are no blue or white pigments in birds.

The study of feather pigments shows very clearly that one and the same pigment may result in very diverse colours. This has been convincingly shown by Orren Lloyd-Jones (1915) in the case of the tumbler pigeon. There is a red-brown pigment of the melanin series, which gives a red colour when it occurs in spherical granules of about 0.3μ in diameter, "plum" colour when the granules are 2μ or more in diameter, and yellow colour when the division is so fine that its granule form cannot be determined. The difference in colour is a question of the microscopical dimensions of the granules of one and the same pigment.

There is in the same pigeon another melanin pigment which under different conditions yields black, dun, blue, and silver colours! In black birds the pigment occurs as spheres 0.5μ in diameter, or as rods 1μ in length, sometimes mingled, sometimes separated. In dun birds the granules are invariably spherical and about 0.3μ in diameter. "Blue" is due to a peculiar clumping and distribution of the pigment in the barbules, and "silver" is due to a similar distribution, but associated with a pitting and roughening of the barbule surface.

According to Lloyd-Jones, all the fundamental self-colours of tumbler pigeons can be accounted for by the interaction of four hereditary factors: R, for red pigment; B, for black pigment; I, for intensity, increasing the amount of pigment produced; and S, for spreading, which apparently means stopping the clumping of the pigment in the middle of the barbule cells.

This investigation is interesting, (1) in showing how very different colours may result from the same pigment (the red or the black), and (2) in illustrating how four hereditary items or factors may by different shufflings of the cards yield diverse final results.

Physical or structural coloration is illustrated in two ways. (a) In some cases the colour changes with the changing light and the position of our eye, the changes of

colour being always in the order of the colours in the rainbow. Such metallic or prismatic colours are well illustrated in Starlings and in Birds of Paradise and in the tail of the Peacock. Abundant pigment, usually dark, is covered by a transparent coating, which seems to act like a number of prisms. These apparently changing colours seem to be restricted to the barbules and usually to those barbules which have no barbicels.

(b) Physical or structural coloration is also illustrated and in great exuberance by those feathers which do not seem to change their colour with the incidence of light or the movement of the observer. All blue and violet colours, all green colours except in the case of turacoverdin, and some bright yellow colours, are of this nature. In most of these cases there is a layer of pigment of some other colour (*e.g.* brown), and outside this there is a colourless layer with a peculiar structure, *e.g.* numerous microscopic ridges. The beautiful iridescence of the pigeon's neck appears to be due (Strong, 1903) to thin-plate interference colours or Newton's rings effects, produced on the dorsal surfaces of the distal portions of the feathers, where spherical pigment granules are in contact with an outer transparent layer. In some other cases the explanation is slightly different. In many yellow feathers, there is no pigment at all; the coloration is purely physical, the surface probably acting like a grating that allows of the reflection of the yellow rays only. This may be seen in some Toucans, Macaws, and American Orioles. In a general way it may be noted that non-metallic structural coloration is distinguishable from pigmentary coloration by the fact that it is at once altered if the surface of the feather be injured. If there is a dark pigment enhanced into a blue colour, or a yellow pigment enhanced into green, the pigment colour will be seen when the feather is held up against a bright light.

Modifications of Colour.—The raw materials of the pigments are brought into the growing feather by the blood which enters the base of the quill; the pigments get their final form inside the living cells of the growing feather;

they are precipitated as granules or held in suspension in saturating oil and fat. Now, it is plain that vicissitudes or changes in the nutritive supply or in the environment may influence the pigmentation of a feather; and the result is technically called an individual *modification*. Something peculiar in the food may result in something peculiar in the pigmentation; thus cayenne pepper affects the colouring of canaries. Or some injury to the young feather may result in the non-deposition of pigment, as we see in the individual white feathers that may occur on a blackbird or crow.

The development of a normal hereditary character (nature) requires appropriate normal conditions (nurture); and the colouring of a bird may depart from what is usual because of something peculiar in the conditions of life. A change in nurture (whether environmental, nutritional, or functional) brings about an internal change that alters the expression that the development of a hereditary character finds.

Fault-bars.—It has been shown by O. Riddle (1908) that what are called "fault-bars," weak areas interrupting the fundamental barring, are due to malnutrition. They may be produced artificially by giving the birds amyl-nitrite which reduces the blood-pressure, or by altering the food disadvantageously. They are usually laid down at night when the blood-pressure is normally low. The dark (melanin) pigment is probably derived from proteins in the blood or in the formative cells of the feather, and the quantity available will naturally vary with the food supply. "The reduced nutrition, brought about daily by the minimum blood-pressure; the disadvantageous position, in relation to the blood, of the pigment and barbule elements of the feather; together with the very rapid rate at which feathers grow, furnish the complex of conditions which bring unfailingly into existence a fault-bar, and, to a more or less appreciable extent, a light fundamental bar, at perfectly regular intervals in the entire length of every feather formation." It is evident that interpretations of

this kind are of high value, for they disclose the primary significance of differences which may subsequently be sifted by some mode of selection.

Variations in Colouring.—Quite different from *modifications* imposed more or less from without are *variations* which arise from within owing to some disturbance in the germ-cells. Thus a true albino without any pigment may arise as a germinal variation; a hereditary factor has dropped out of the inheritance. Perhaps it is the factor for the pigment-forming substance (the chromogen); perhaps it is the factor for the ferment which must operate upon the chromogen before the pigment can be produced.

Similarly, melanistic variations appear to be of frequent occurrence, where there is a superabundance of dark pigment. A darkening of the plumage might of course be an individual modification, but there are cases where the darkening is seen in a large section of a species, and here we have probably to do with the result of germinal variation.

Albinism.—There are many records of albinism or absence of pigment in birds. It may be total, but it is more frequently partial. When total, it implies that the hereditary factor or factors for pigment production must have dropped out of the inheritance. In some cases, at least, there is a factor for the pigment-producing material, or chromogen, *e.g.* tyrosin, and a factor for the ferment which activates the chromogen, *e.g.* tyrosinase. When partial, it may mean a general deficiency in the pigment available or in ferments required to give the pigment-forming material its coloured expression. When very local it may mean nothing more than a disturbance in the normal blood-supply of a certain area of growing feathers. Albinism is not to be confused with normal whiteness, in which different pigment factors neutralise one another in expression.

Albino blackbirds, crows, sparrows, and swallows are well known. L. Petit has collected a number of rarer cases (1909), *e.g.* an eared grebe with all the dorsal surface dull white, a cream-coloured (isabelline) woodcock, a partridge of the same colour, a blackbird covered with white

spots, a perfectly white tree-pipit, a white and greyish-white sand-martin. A white coot with normal eyes has been described; the whole plumage was snowy white except a few ashy feathers at the end of each wing.

The putting on of white plumage in the ptarmigan illustrates a constitutional rhythm corresponding to an external periodicity; but it is not to be supposed that the cold of winter is directly responsible for making the new feathers colourless. The cold acts as a stimulus to a pre-established rhythm. The difference between *new* white feathers and their coloured predecessors is that gas vacuoles take the place of pigment granules, the whiteness being due to the reflection of the light from a multitude of internal surfaces, as in the case of foam. According to Metchnikoff (1906), a coloured feather in ptarmigan and willow grouse may be changed into a white feather by the activity of wandering amœboid cells (chromophagous) which transport the pigment into the skin.

An interesting little point is that when pigment is quite absent (in albinos), the structural specialisation so frequently involved in the production of colour effect is also absent (Chandler, 1916).

Physiological Meaning of Pigments.—Hæmoglobin has obviously a fundamental physiological significance as an oxygen-capturer and carrier, but its colour plays no part in this significance. Hæmocyanin which is also a common oxygen-carrier in invertebrate types is faintly blue.

It is possible that some superficial pigments of a dark colour have a protective value against the ultra-violet rays of sunlight.

It is possible that some pigments are of value in relation to the regulation of temperature in the body, just as the absence of pigment in the winter plumage of the ptarmigan gives that bird the dress physiologically most economical.

It is certain that dark pigment is of use in making the eye a dark chamber, and the changes in the pigments of the retina have some direct significance.

Apart from such suggestions, what can we say at present

save that pigmented substances may be waste-products, or reserve-products, or by-products of the bird's metabolism?

The External Uses of Colour.—Without admitting that it is incumbent on the naturalist to show the utility of all the details of coloration, we are free to recognise that colour may often be of use. Let us first of all collect the utilitarian suggestions in one paragraph. (1) Coloration may give the bird a garment of invisibility, of special value during incubation or when feeding on the ground. It may break up the bird's body so that it becomes a difficult target for the hawk. (2) Coloration may assist in the recognition of kin by kin, of the parents by the young, or of one sex by the other. (3) Rather different is Mr. Pycraft's suggestion that the bright colours sometimes seen around or in the mouths of nestlings may serve as a guide to the parents when rapidly feeding the young. (4) Coloration may be a factor in the *ensemble* of attractiveness that stimulates sex-interest and sex-excitement, and makes pairing more effective.

It is on general grounds probable that there are primary physiological reasons for certain types of pattern in plumage. Just as the lie of the hair in particular parts of different mammals is probably dependent to begin with on the conditions of muscular strain, blood supply, and innervation in different areas of the skin, so it may be with the lines along which feathers develop in birds. But this is not inconsistent with adaptive variations within the prescribed limits being established by selection, whether natural or sexual.

Similarly, in regard to the deposition of pigment, there may be physiological conditions which determine centres of pigment formation or deposition in the skin, while adaptive variations within the prescribed limits are established by selection. Colour patterns in birds have been studied by Glover M. Allen (1914), who lays stress on the idea of centres from which pigment formation begins and spreads. A reduction in the area covered by any of these primary patches results in a white mark at the line of junction with another, constituting a "primary break." The patches

include a median crown patch, and five paired patches—corresponding to the ear, neck, shoulder, side, and rump. These are physiologically independent of each other, and may have different colours. He claims that in some wild species the formation of these white markings may be seen in gradual progress, complexifying the pattern. The converse of this centrifugal pattern-making is also to be seen, as in the special pigmentation of extremities. One cannot go far at present with these theories, but that is no reason for not thinking over the physiological conditions that may underlie the heterogeneous pigmentation of different parts of the body.

The general point we wish to make is this: there is reason to believe that the familiar cross-barring of the feathers of some hawks is primarily related to a diurnal fluctuation of blood-pressure. When the feather is a-making and pigment is being deposited in the cells, the fluctuations in the blood-pressure result in the bars, which are the ripple-marks of growth. But this is not contradictory to the idea that there might be an adaptive advantage in the cross-barring, such as some would find in the cuckoo's breast feathers being rather hawk-like.

The interpretation of distinctive markings affords attractive opportunity for biological ingenuity, but it is not easy to win conviction except in cases where the field observations of competent and critical naturalists are unanimous. A good instance of uncertainty may be found in the case of white markings. (a) Sometimes in relation to darker upper parts a white area may make a bird very inconspicuous, and we say "concealing coloration" or other words to that effect. (b) Sometimes the white patch is flaunted, exposed in flight, and we say "a sight clue for kin." (c) Sometimes, as in the wheatear, the white patch is very much in the rear, so that, as we say, the hawk's thrust grips only feathers. (d) Sometimes the whiteness is all underneath, and is not much seen except when the male makes a banner of his wings within the range of his desired mate's vision, and then we say "preferential mating" or

“sexual selection.” Now, each and all of these interpretations and others more subtle still may be quite legitimate; our only caveat is that their acceptance should not be on too easy-going terms. We must remember, for instance, as is well explained by H. C. Tracy (1910), that striking coloration may develop for purely physiological reasons under conditions of comparative immunity from attack, and may prove a rather embarrassing legacy in subsequent ages when the conditions have changed.

Utilitarian interpretations are not convincing without experiment, but there is no reason whatever for severely refusing to *consider* the utility of coloration, especially as the consideration may suggest experiment. From a paper by Dr. J. C. Mottram (1916) we take a utilitarian classification which had primary reference to Lepidoptera.

COLOUR AND PATTERN	UNRELATED TO THE VISUAL PERCEPTION OF OTHER ANIMALS	For the absorption of Light Rays. For the absorption of Heat Rays. Excretory Products, etc.	
	RELATED TO THE VISUAL PERCEPTION OF OTHER ANIMALS	INCONSPICUOUS TO OTHER ANIMALS	To the eyes } Protective of enemies } coloration
			To the eyes } Coloration of prey } concealing attack
		CONSPICUOUS TO OTHER ANIMALS	To the eyes } ? of friends }
			To the eyes } Attracting and of enemies } repelling and warning co- loration
	To the eyes } To allure of prey }		
To the eyes } Social signals of friends } Sexual signals			

In some cases the protective value seems indubitable. Thus a careful ornithologist, Dr. F. M. Ogilvie, confessed that he never himself found a very young nestling Ringed Plover, though he often looked for them and knew them from specimens obtained by hatching eggs out in an incubator. " Yet, I have constantly been over ground where I knew the birds were breeding freely, and where nestlings must have been quite plentiful." The invisible young birds are stone-coloured, with black-tipped down. " As long as the parents are uttering their alarm note, so long will these little fluffy balls, only hatched perhaps a few hours ago, remain squatted and motionless, with their necks stretched out, their bodies buried in the golden moss, so that all the lighter underparts, including the light eye streak, are hidden from view."

CHAPTER III

ADAPTATIONS OF THE BIRD'S SKELETON

1. Lightness and Tendency to Fusion. § 2. Adaptations to Flight.
- § 3. Adaptations to Bipedal Progression. § 4. Adaptations of the Skull. § 5. Adaptations in the Backbone. § 6. Muscular System.

WHEN the term "adaptation" is used to denote a result and not a process, it means a special adjustment of structure or function to meet particular conditions of life. The fundamental qualities of living creatures are adaptive in the wide sense, for they make for the continuance of the organism in the midst of an inanimate environment, which includes, to say the least, many disintegrative influences. But the term adaptation is convenient to denote less fundamental and more detailed adjustments. The wall of the food-canal is adaptive in so far as it is capable of absorbing the food; it would not be worthy of the name of food-canal if this were not so; but the term "adaptation" is conveniently restricted to a particular adjustment such as the presence of thousands of finger-like villi projecting into the cavity, which greatly increase the internal absorbing surface.

Similarly, bone is a supporting tissue and as such adaptive to the continuance of a large and heavy animal. Especially on land, a bony skeleton, or some other kind of skeleton, becomes indispensable. But it is convenient to keep the term "adaptation" for particular adjustments of the bony skeleton, for instance, in its internal architecture which is adjusted to stand definite strains and stresses, and often shows remarkable economy in the use of material. Still more appropriate is the use of the word "adaptation" when out of a generalised structure, suited for varied uses, a

specialised structure has been evolved suited for overcoming particular difficulties in the conditions of life. Whatever interpretative theory of evolution is accepted, the general fact seems clear that adaptations are the results of long processes of gradual improvement in efficiency.

§ I. LIGHTNESS AND TENDENCY TO FUSION

Lightly Built.—The skeleton of the bird is lightly built, affording a relatively large surface for the insertion of muscles without the corresponding increase of weight that would be involved if the bones were as substantial as those of a reptile or a mammal. The skeleton is built on the hollow girder principle. The long bones have large medullary cavities, and many bones of many birds contain prolongations of air-sacs from the lungs. The marrow often disappears entirely at an early age; and while the bone is still a-making an air-sac enters its cavity. In some birds, like the albatross, practically every bone is "pneumatic" except the scapula and the hyoid. In the case of skull-bones the air-cavities are in communication with the nasal chamber and auditory passage, not with the lungs. But although the bones are not massive, they are not in any way weak. There is a hard dense cortex, which does not attain great thickness, and below this comes a framework of spongy texture, especially marked in Running

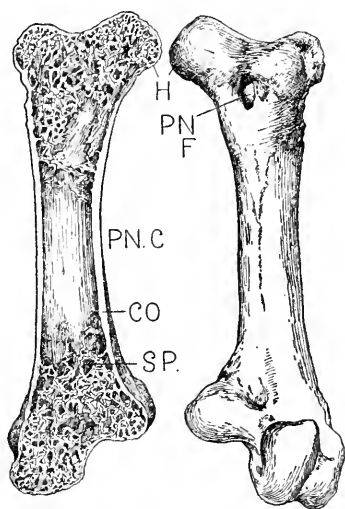


FIG. 5.—Thigh-bone or femur of an ostrich, cut open to left. From a specimen. H., head of femur, which works in the hip-joint or acetabulum; PN.F., pneumatic foramen, where air-sac enters; PN.C., pneumatic cavity; CO., dense cortex; SP., spongy texture.

Birds. Architectural experts say that the beams of this framework are disposed so as to give strength to the bone as a whole, enabling it to stand the wonted strains and pressures. Some of the most pneumatic of birds, such as the hornbills, are poor fliers, and one cannot regard the pneumaticity as essential to powerful flight; nevertheless, other things equal, the pneumaticity and the hollow girder architecture must make flight easier, and may be regarded as adaptive.

Tendency to Fusion.—A second general character of the bird's skeleton is the tendency that adjacent bones have to fuse together while still in the making. What is behind this tendency we do not know; it must express a general constitutional peculiarity, for it occurs in so many different parts of the skeleton, *e.g.* the skull, the thoracic region of the backbone in flying birds, the sacral and adjacent regions, the end of the tail, the region of the wrist and hand, and the ankle. It is possible to show the advantage of these fusions, as we shall proceed to do, but a tendency so widespread must surely rest on a constitutional peculiarity. Such compound bones as the carpo-metacarpus and tarso-metatarsus are absolutely distinctive of birds, never occurring elsewhere. But a coalescence of bones sometimes occurs as a pathological variation in other classes. In Running Birds the bones of the skull are for a long time incompletely fused, and the vertebræ of the thoracic region remain free. On the other hand, in these same Running Birds there is a fusion of scapula and coracoid, which does not occur in Flying Birds. It may be noted that while one of the methods of evolution is to multiply the number of separate parts in a structure, as may be illustrated by the presence of over 200 vertebræ and pairs of ribs in some snakes, another method is to reduce the number of separate parts, and this is seen in the tendency to fusion exhibited by adjacent bones in the bird's skeleton. The terminal caps or epiphyses characteristic of mammals are not seen in birds.

§ 2. ADAPTATIONS TO FLIGHT

(1) In adaptation to flight the thoracic vertebræ are fused (with a few intelligible exceptions), and this fusion helps to afford a firm fulcrum for the action of the wings in striking the air. The wing works against the pectoral girdle, with the coracoid bone braced on the breastbone, and the shoulder-blade (scapula) bound by ligaments to the ribs and to the backbone. There is a coherent springy framework formed of backbone, breastbone, ribs, and pectoral girdle; and against this the wing has its leverage. A mobile vertebral column in the thoracic region would be quite inconsistent with vigorous flight, and it is interesting to notice that there is a tendency to coalescence of dorsal vertebræ in bats. In Running Birds there is no thoracic fusion.

(2) In adaptation to flight, the breastbone or sternum has in most cases a keel or carina, which serves for the insertion of the pectoral muscles. The absence of the keel in Running Birds, and its degeneracy in the New Zealand burrowing parrot *Stringops*, may be readily interpreted. The strength of the keel in the flightless penguins is intelligible enough when we remember how much they use their fore-limbs in swimming. A breastbone or sternum is a bilateral structure, arising in development from a coalescence of the ventral ends of the ribs, and each side contributes one side of the keel. This makes it easier to understand how it is that in the crane and the whooping swan, the windpipe descends into the keel and bends up again.

It is interesting to notice that there is a keel on the breastbone of bats and also in moles, both in relation to the strong pectoral muscles for flying in the one case, for burrowing in the other. In the extinct *Pterodactyls* there was sometimes a slight keel; but, apparently, never more than slight.

There is on the whole a correlation between the strength of the keel in proportion to the rest of the breastbone and

the power of flight. The strong development of the keel and of the breastbone as a whole may be associated with a characteristically avian lightening of the bone, and with

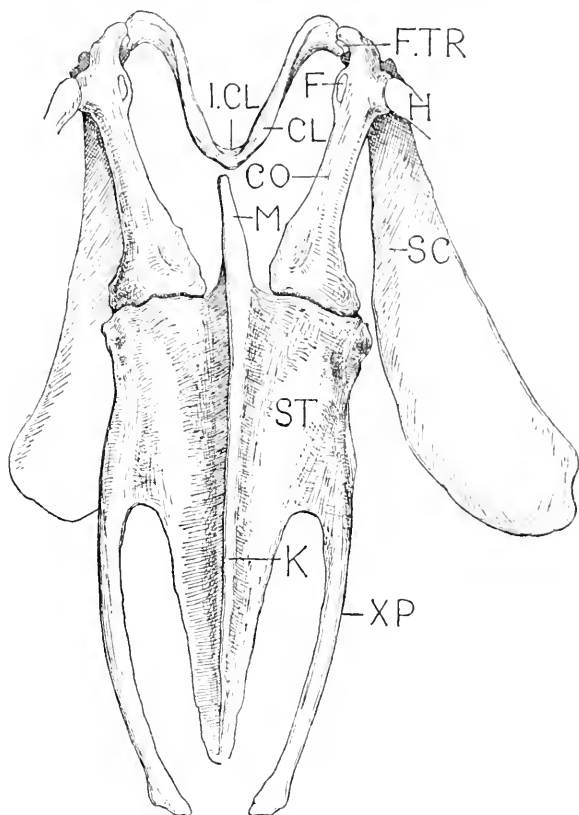


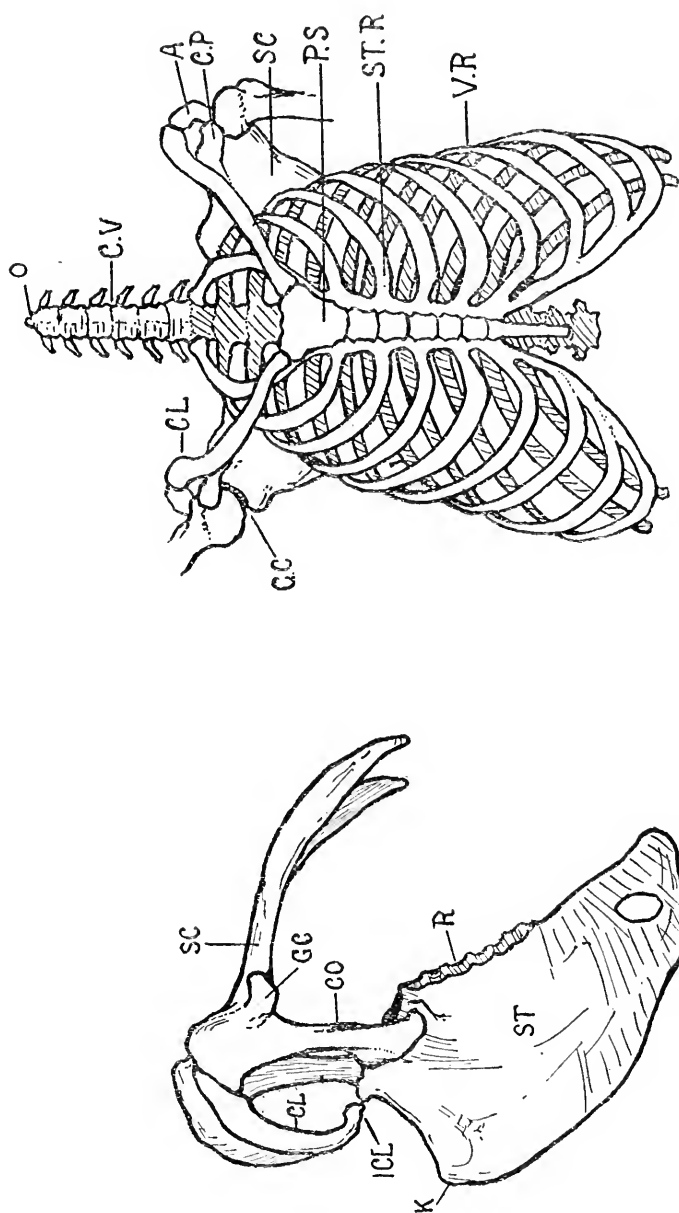
FIG. 6.—Breastbone and pectoral girdle of a penguin. From a specimen. ST., sternum; K., keel; XP., xiphoid process of sternum; M., manubrium or anterior process of sternum; sc., scapula or shoulder blade; CO., coracoid; F., foramen in coracoid; H., head of humerus working in the glenoid cavity where scapula and coracoid meet; F.TR., foramen triosseum bounded by scapula, coracoid, and clavicle—a pulley hole for the tendon of a pectoral muscle; CL., the clavicle; I.CL., interclavicle.

its splitting up into (xiphoid) processes. Another adaptive feature is that the backward elongation of the breastbone forms a useful supporting floor for the abdominal viscera—

of especial value in flying and swimming birds. In the Running Bird the breastbone is a broad shield, not extending far back, but the weight of the viscera in the Running Bird is borne by the strongly developed dorsal and lumbar vertebræ, and by the backward extension of the rib-framework.

It stands to reason that a keel should be absent or vestigial in the Running Birds, and it is interesting to find that it should be degenerate in the New Zealand parrot (*Stringops*) which has ceased to fly and taken to burrowing. But when we get beyond recording an intelligible correlation between a degenerate keel and little capacity for flight, we get into difficulties. Is the degenerate state of the keel in *Stringops* the cumulative inherited result of an abandonment of flying? Or was there a germinal variation in the direction of degenerate keel which led the bird to be sluggish in flight? Or, given an exploiting of a new kind of habit and habitat, is the reduction of the keel a result of an economical variation in the disposal of skeletal material, and of a cessation of that persistent sifting which seems to be sometimes necessary to keep a variable structure up to the level of efficiency? Few naturalists will be inclined to dogmatise as to which of these answers is nearest the true interpretation, but the balance of evidence at present is strongly against the first.

(3) In adaptation to flight there is a very firm attachment of the pectoral girdle. The lower ends of the coracoids fit into deep grooves on the anterior margin of the sternum; the upper ends are strongly bound to the front end of the scapula by ligaments. The sabre-like scapula is lashed by ligaments to the dorsal surface of the ribs along which it lies. The glenoid cavity where coracoid and scapula meet is well suited for the free action of the head of the humerus; it admits of free play for the wings. The spring-like merrythought (clavicles and an interclavicle) forms part of the fulcrum against which the wings work; it is bound by ligament to the front of the sternum, and the interclavicle is sometimes fused to the tip of the keel. If the merrythought is broken, the bird cannot fly. It is



FIGS. 7 and 8.—Comparison of breastbone and pectoral girdle of bird (to the left) and of an ape (to the right). SC., scapula; CO., coracoid; G.C., glenoid cavity where the humerus articulates; CL., clavicle; I.CL., interclavicle; ST., sternum; R., notches where ribs articulate; K., keel of the sternum. O., odontoid process on axis or second vertebra; C.V., cervical vertebrae; A., acromion process of the scapula; C.P., coracoid process, fused to the scapula; PS., prasternum, the front of the breastbone; ST.R., sternal parts of the ribs, reaching to the breastbone; V.R., vertebral parts of the ribs; G.C., glenoid cavity for the head of the humerus, it is formed by the meeting of scapula and coracoid.

rudimentary or absent in Running Birds ; it is rudimentary in some birds that do not fly much, *e.g.* certain parrots. The very strong coracoids also form a part of the fulcrum for the stroke, and along with the merrythought they must also protect the heart against compression. Of great importance is the way in which breastbone, pectoral girdle, ribs, and thoracic vertebræ are all bound together into a coherent elastic basket, on which the wings work ; the compression of this basket, as the backbone is lowered and the breastbone is raised, affects the lungs, which are firmly attached to the ribs, and thus *flying helps breathing*. Hilzheimer calls attention to the mobility of the joint between the coracoid and the breastbone in humming birds, and connects it with the rapidity of the wing-strokes. It allows of an unusually marked and rapid expansion and compression of the body-cavity, thus facilitating respiration.

(4) A very clear instance of adaptation is seen in the relation of the elevator muscle of the wing to the breastbone on the one hand and the humerus on the other. This muscle that raises the wing—the pectoralis minor—is inserted on the ventral surface of the breastbone. How can it, lying ventrally, by contracting, raise the wing, which is high above it ? How can a sailor on the deck of a ship pull a sail upwards by hauling a rope downwards ? Obviously, the rope must work over a pulley, and so is it in the case of the tendon of the muscle. It passes upwards alongside of the coracoid to the *foramen triosseum* (to the internal side of the shoulder-joint), where scapula, coracoid, and clavicle touch one another and enclose a hole. The tendon passes through this *pulley hole* and is attached to the dorsal surface of the humerus. Thus when the muscle down below contracts, its tendon pulls the wing up.

(5) In adaptation to flight remarkable changes have come about in the skeleton of the fore-limb. There is greatly reduced mobility in the different parts and the wing works as a unified whole. When at rest the wing forms a compressed letter Z, the elbow pointing backwards, the wrist joint forwards, the tips of the three digits (probably

I, II, and III) backwards. The three parts of the wing—the upper arm (humerus), the fore-arm (radius and ulna), and the hand (carpo-metacarpus and digits)—move *in one plane in relation to one another*, as the blade of a pocket-knife in relation to the sheath. Running along the front of the wing from the upper arm to the lower arm there is a

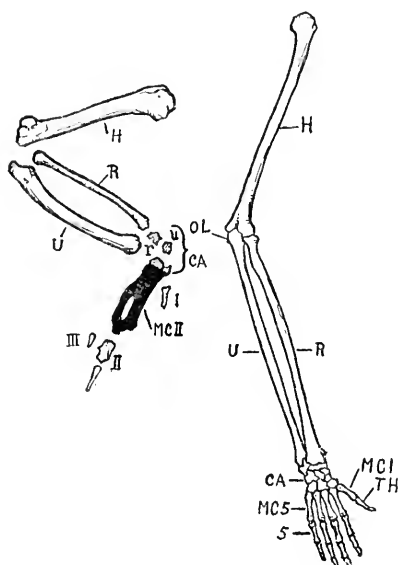


FIG. 9.—Comparison of bird's wing and monkey's arm. H., humerus; R., radius; U., ulna; *r.*, in bird, radiale, a free wrist or carpal bone; *u.*, in bird, ulnare, the other free wrist or carpal bone; CA., the carpal region or wrist; I., the phalanx or joint of the bird's thumb; MCII., metacarpal of second digit, forming part of the peculiar bone, the carpo-metacarpus, which is characteristic of birds; II., the second digit of the bird, with two joints or phalanges; III., the third digit of the bird with one joint; the metacarpal part of the carpo-metacarpus is equivalent to three palm bones and is marked solid black, the distal carpals are fused to it, and are touched by the radiale and ulnare; OL., on the monkey's arm is the olecranon or elbow process of the ulna; MC.I., the metacarpal of the thumb (TH); MC.5, the metacarpal of the little finger (5).

slight web or patagium with an elastic band (*tensor patagii longus*) which is shorter than the bones of the wings and thus prevents their complete extension. The whole adjustment is complicated, but the net result is to reduce the

mobility of the parts of the wing, to make the wing act as one instrument when it strikes, and to tuck it up when at rest in a space-economising fashion—especially useful when the bird is swimming with its feet.

The radius and ulna are quite free from one another, but they do not move on one another except that in the folding up of the wing the radius moves forward a little on the ulna and thus helps to bring the hand into its resting position.

The embryo bird shows four or five wrist-bones or carpals; but these are reduced to two free bones—the radiale and the ulnare. This is in relation to the reduced mobility of the whole limb. What becomes of the other carpals? Three of them fuse on to the three fused metacarpals, forming the compound bone known as the carpo-metacarpus. This may be described as consisting of *half of the wrist and the whole of the palm*. It affords the firm foundation for the primaries—the longest feathers of flight. At its upper end it bears the single joint or phalanx of the thumb; at its lower end it bears the second digit with two joints, and the third digit with one.

There is some uncertainty in regard to the digits that are now represented in the bird's wing. Some authorities say that the strongest one is the third, and that those on the two sides of it are the second and fourth. In other words, the first and fifth have disappeared. We adhere to the interpretation of the bird's three digits as I, II, and III. But the important fact is that the bird's hand is relatively rudimentary. It has been sacrificed to making a wing—that is to say, a unified basis for the pinions.

(6) In the oldest known bird, Archæopteryx, there was a long tail like a lizard's, with a very peculiar arrangement of feathers in a row on each side. Such a tail doubtless had some use as a steering organ. In modern birds the tail in the strict sense is always short, and in Flying Birds it ends in a fusion, the ploughshare bone or pygostyle. If there seems to be a long tail in a living bird, as in the pheasant, it is always a *feather* tail. The ploughshare bone may be

ranked as an adaptation, for it affords insertion to the tail feathers or rectrices, which can be used as a brake in flight, or by being suddenly raised or lowered may enable the bird to avoid a telegraph wire or the like. The actual steering in a flying bird is effected by the differential action of the wings and in some measure by tilting the body by means of the wings. Anatomically, the pygostyle may be

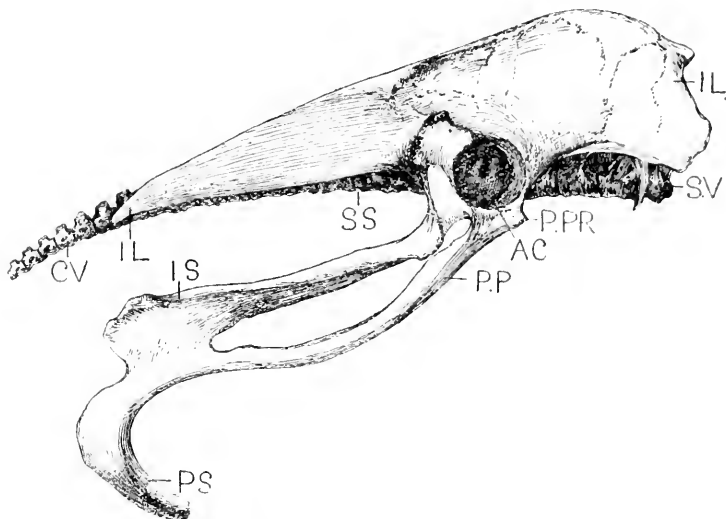


FIG. 10.—Pelvic girdle and sacral region of an ostrich. From a specimen. IL.—IL., beginning and end of the ilium; IS., ischium; P.P.R., pectineal process; AC., acetabulum; P.P., post-pubis; P.S., pubic symphysis, peculiar to the ostrich; s.v., sacral vertebrae; ss., syn-sacrum; c.v., free caudal vertebrae.

distantly compared with the coccyx, a post-sacral fusion of vertebrae in man and anthropoid apes, and, also remotely, with the urostyle or post-sacral fusion of vertebrae in the frog. It is interesting to find that the ploughshare bone is particularly large in birds with strong tail feathers. This may be well seen in the woodpecker, where the tail feathers serve as a prop in climbing a tree. This illustrates functional adaptation. But it does not follow that the usage of the feathers made the pygostyle large.

§ 3. ADAPTATIONS TO BIPEDAL PROGRESSION

If a perpendicular be dropped from the hip-joint (acetabulum) where the thigh-bone (femur) articulates with the hip-girdle, it will be seen that in most birds a large portion of the body lies in front of this. In man's case the anterior part of the body is in line with the vertical axis of the leg. In the old man's stoop the muscles that keep the anterior part of the vertebral column vertical are losing their tone. In adaptation to the condition of affairs in birds the ilia are much elongated in front of and behind the acetabulum, and are fused to a long stretch of vertebræ—the syn-sacrum. This gives the hip-girdle *a long and strong grip of the backbone*, obviously facilitating the balance of the body on the apex of the leg. The risk of toppling forward is obviated.

The syn-sacrum has a complex make-up. It consists of two or so thoracic vertebræ (bearing ribs), all the lumbar vertebræ, the two true sacrals which in the embryo are first connected with the girdle, and, finally, about half of the caudals. Beyond it, posteriorly, there project the free caudals ending in the ploughshare bone in Flying Birds. The formula of the syn-sacrum for the pigeon is: Thoracics, 1; +Lumbar, 5 or 6; +Sacrals, 2; +Caudals, 5—a dry detail at first sight, but eloquent when we appreciate the mechanical significance of the complex coalescence.

It is very instructive to contrast the bird with an animal like the frog, which does not and could not stand on its hind legs. In the frog there is only one sacral vertebra, and the tips of the long ilia are connected to its transverse processes by a loose ligamental union, an arrangement well-suited for swimming and spasmodic leaping. In the bird there are over a dozen "sacral" vertebræ and the ilio-sacral connection is a fusion, an arrangement well-suited for bipedal progression. It need hardly be said that in thinking of such problems one must get beyond the

dead skeleton to the living skeleton enswathed in living muscle and bound together by living tendons. When in walking we rest for a brief moment with one foot on the ground and swing forward the other leg, we are balancing the body on the smooth head of the thigh-bone fitting into the socket of the hip-girdle, and in this balancing alone over a score of muscles are implicated. Similarly, of course, with the Running Bird.

One is tempted to regard the pectineal process in front of the acetabulum of birds as a relic of a true pubis, the pubic bar of birds being then interpretable as the post-pubis of some extinct reptiles. But as regards the pectineal process, this theory does not work out well, as Lebedinsky (1914) points out clearly. Parker and Baur have shown that the pectineal process of the kiwi is formed by both ilium and pubis; Lebedinsky has shown that the pectineal process of the African ostrich is formed from the pubis only; Burge, Mehnert, and Lebedinsky have shown that the pectineal process of *Carinatae* is formed from the ilium only. With so much heterogeneity of origin, the pectineal process cannot have any historical (phylogenetic) importance. It is probably a new acquisition within the class of birds; it serves for the insertion of the ambiens muscle—of some use in perching—when that muscle is developed.

There are other peculiarities of the hip-girdle besides the length of the ilia on each side of the acetabulum and their thorough fusion to the complex syn-sacrum, but their interpretation is more difficult. The backward-going pubic bar is perhaps homologous with the post-pubis of some reptiles. The ischia are firmly fused to the ilia. The whole hip-girdle with its six or more component bones is one piece. There is no ischiac symphysis except in the American Ostrich (*Rhea*) and no pubic symphysis except in the African Ostrich (*Struthio*). It may be that the suppression of the true pubes (on one view) or the backward turning of the true pubes (on another view) is adaptive to the fact that birds lay relatively large hard-shelled eggs which cannot be safely subjected to pressure.

The salient features of the skeleton of the bird's leg are the elongation of the different regions, the more or less vertical position of the instep region, and the reduction of the number of separate bones. The thigh-bone has a conspicuously defined round head, working deeply and freely in the acetabulum; the fibula is reduced to an incomplete splint, which may be partially fused to the tibia; the upper or proximal row of ankle-bones or tarsals has coalesced in embryonic life with the lower end of the tibia, forming a tibio-tarsus, which is peculiar to birds; the lower or distal row has coalesced with the upper end of three (in the ostrich, two) fused metatarsals, forming a tarso-metatarsus, which is also peculiar to birds. Thus the adult shows no free tarsal bones, but they are clearly seen in the unhatched bird; and in a true, not merely courtesy, chicken on the table it is easy to separate an imperfectly ossified piece from the lower end of the tibio-tarsus and the upper end of the tarso-metatarsus. These separable pieces correspond to the two rows of tarsal bones. When a bird moves its ankle-joint it is really moving the upper tarsals against the lower tarsals, the interest of which is that it corresponds to the reptilian inter-tarsal movement. This inter-tarsal ankle-joint of reptiles and birds is in

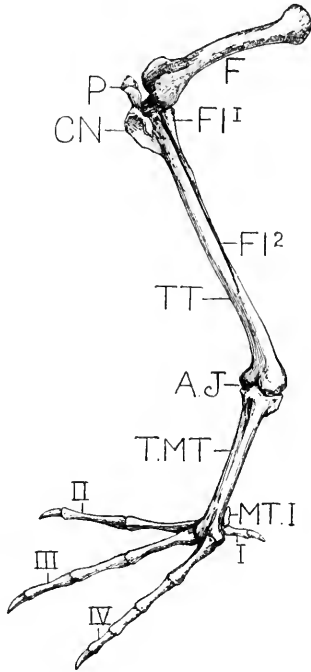


FIG. 11.—Fowl's hind-leg. From a specimen. F., femur; P., patella or knee-pan; C.N., cnemial crest on the tibio-tarsus (T.T.); FI.¹, the head of the fibula; FI.², lower end of the tapering incomplete fibula; A.J., the ankle joint; T.M.T., tarsometatarsus; MT.I., the first metatarsal, quite free; I.-IV., the toes.

marked contrast to the cruro-tarsal ankle-joint of mammals. For when a mammal moves its ankle-joint, the lower end of the tibia works against one of the upper tarsals, the astragalus, and to a slight extent against the other, the calcaneum or os calcis. The last-named bone which projects so conspicuously at the heel of the mammal is equally conspicuous by its absence in the bird. Yet it is there all the time.

The adaptations in this part of the skeleton are three. (a) The suppression of the separate tarsals, which usually occur in two mobile rows, makes it easier for the bird to recover its balance when it suddenly alights on the ground or on a perch. (b) The almost vertical position and the length of the tarso-metatarsal region (half of the ankle and the bulk or the whole of the instep) facilitate the sudden upward and forward spring when the bird launches itself into the air. (c) The fusion of three metatarsals (two in the ostrich) into one long bone is comparable to the fusion of the third and fourth metatarsals (or metacarpals) in the leg of a cow; it makes a firm step and a strong spring easier, it simplifies the disposition of the tendons, and it lessens the risk of dislocation and sprain. It is interesting to notice the partial separateness of the lower ends of the three metatarsals in the penguins, where the hind leg serves in great part as a propeller. Hilzheimer points out that this is a secondary peculiarity, for the fossil penguins are nearer the usual type as regards their metatarsals. In divers and grebes the tarso-metatarsus is laterally compressed like a blade, an adaptation to reduction of friction in swimming, and concentrating the stroke in the toes which form the instrument that strikes the water.

The maximum number of toes in a normal bird is four, of which the first is the hallux or big toe. If there be four, the metatarsal of the hallux is free from the other three fused metatarsals and is turned backwards. If there are only three toes, the hallux has been suppressed. The obvious general adaptation in the majority of cases is the elongation and horizontal spreading out of the toes, affording

a grip of the ground or of the perch, and also abetting the leap into the air. But special adaptations are numerous. The toes of the Jacana are greatly elongated, well suited for walking on leaves in the water, and something of this is seen in the Water-hen. Two of the toes of the cuckoo are

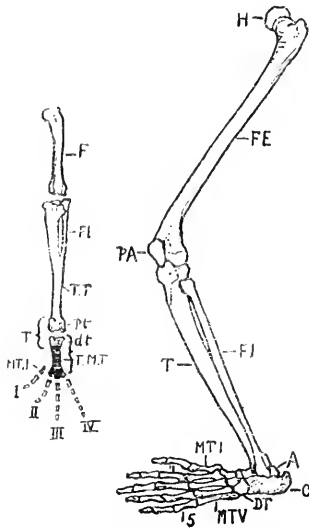


FIG. 12.—Comparison of bird's leg and ape's leg. F., femur; FI., fibula, a mere splint in the bird, complete in the ape; T.T., tibio-tarsus in bird, i.e., tibia plus the distal tarsals; T., tibia of ape; P.T., proximal tarsals of bird, fused on to the base of the tibia; A. and C., astragalus and calcaneum in ape, the proximal tarsal; *d.t.*, the distal tarsals of the bird, fused on to the top of the three fused metatarsals, making the tarso-metatarsus, peculiar to birds; T., in bird, the tarsal region, the metatarsal portion is represented solid black; MT.I., in the bird, the first metatarsal, free by itself; I.—IV., the bird's toes; D.T., in the ape, the distal tarsals; MT.I., in the ape, the metatarsal of the big toe; MT.V., the metatarsal of the little toe (5); PA., patella or knee pan.

turned forward and two backward, the better for gripping the perch. In the swift they are all turned forwards, which is well suited for clinging to the nest.

In some old-fashioned birds, such as divers, there is a strong upward prominence, often about an inch long, rising above the upper end of the tibia at the knee-joint. It serves for the insertion of muscles and helps in the strong

swimming stroke of the hind leg. It occurred also in strong development in the extinct toothed *Hesperornis*, a sort of giant loon, of the Cretaceous period. Now it is an interesting technical point that this knee-process, which has the same appearance and the same functional significance wherever it occurs, is structurally of three different types. (a) It may be a huge patella fused to the upper end of the tibia, which shows only a small cnemial crest. This is the case in *Hesperornis*. (b) It may be a prolongation of the cnemial crest of the tibia which has fused with a large patella. This is the case in Grebes. (c) It may be an exaggerated cnemial crest with a mere scale of a patella. This is the case in Divers.

§ 4. ADAPTATIONS OF THE SKULL

Much follows from the fact that the bird has surrendered its hand in the making of the wing. This involves a utilisation of the skull in a notable way as a manifold instrument, *e.g.* for seizing the food, for reaching to the ground, for hanging on by, for manipulating the nest materials, and for preening the feathers. In some cases, of course, the feet have taken on hand duties, as when the osprey seizes the trout in its talons. What cranial peculiarities can be interpreted as adaptive ?

(a) The early fusion of most of the bones in Flying Birds, a fusion so thorough that boundaries are often quite obliterated, makes the skull more of a unified instrument. This may often be an advantage, as in the case of the woodpecker which uses its skull as a hammer. The movable bones of the bird's skull are the lower jaw, the quadrate on which it works, the rod-like columella running from the drum of the ear to the inner ear, and the hyoid supporting the muscles of the tongue. But the pterygoids on the roof of the mouth usually articulate freely with the basisphenoid ; the lachrymals in front of the orbit may remain free ; and there is often a flexible region—almost a joint in parrots—where the beak joins the frontals. It is interesting to

notice the fusion of skull bones in the extinct flying Pterodactyls, which do not seem to be related to birds.

(b) Very characteristic is the exaggeration of the premaxillæ which form the bulk of the beak, and the absence of teeth in modern birds is compensated for by the very effective horny bill.

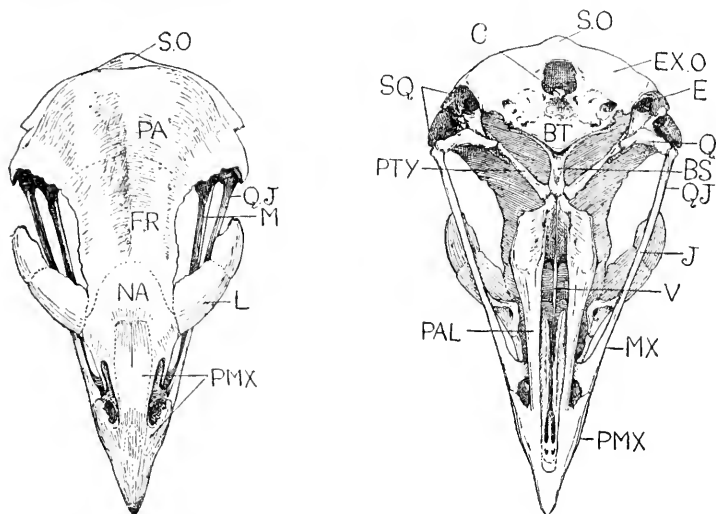


FIG. 13.—Dorsal and ventral view of a bird's skull. From a specimen. S.O., supra-occipital; PA., parietal; FR., frontal; NA., nasal; PMX., premaxilla; L., lachrymal; Q.J., quadrato-jugal; M., mandible or lower jaw. C., occipital condyle, formed from the basi-occipital; EX.O., exoccipital; E., ear-hole; Q., quadrate; SQ., squamosal; B.T., basi-temporal; PTY., pterygoid; MX., small maxilla; v., vomer; J., jugal; BS., basi-sphenoid.

The alleged hints of a dental system in birds are probably altogether mistaken. "Tooth-papillæ" have been described in embryo parrots, but they are mere analogues of teeth, with no relation to true dental primordia. The dental ridges of Röse are connected with the development of the horny bill. According to Hide (1912), who has gone carefully into the question, there is not in birds any trace of a dental ridge or of dentine.

The minute structure of the egg-tooth has been carefully studied by B. Rosenstadt (1912), who finds that the

entire cells—including the nuclei—of an epidermic thickening are changed into horny fibres, running longitudinally, transversely, and perpendicularly. In the formation of the ordinary horny covering of the beak, it is only the mantle of the epidermic cells that is changed into the horny fibre, and more or less thin plates result. The egg-tooth and a corresponding rudiment on the tip of the mandible appear earlier than the horny bill, and, as has been stated, their mode of cornification is different. It may be, Rosenstadt suggests, that they represent an old-fashioned armature of the jaws, older than the modern horny bill.

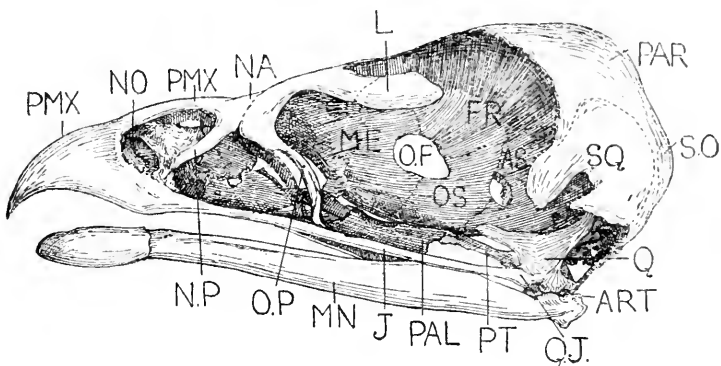


FIG. 14.—Side view of bird's skull. From a specimen. PAR., parietal; S.O., supra-occipital; SQ., squamosal; Q., quadrate; FR., frontal; AS., ali-sphenoid; OS., orbitosphenoid; O.F., optic foramen; ME., mesethmoid; L., lachrymal; NA., nasal; PMX., premaxilla; NO., nostril; N.P., nasal process of premaxilla; O.P., orbital process of frontal; J., jugal; PAL., palatine; PT., pterygoid; Q.J., quadrato-jugal; ART., articular of the lower jaw or mandible (MN).

(c) The complex lower jaw is made up of six bones on each side, thus revealing affinity with reptiles and marked contrast to mammals (where the mandible is simple), but from the present point of view it is more interesting to notice its loose articulation with the movable quadrate, for this increases the gape—an important point when the food has to be swallowed without chewing and without too many questions in regard to size. With the absence of any mastication we may associate the slenderness of the infra-

temporal bar (made up of jugal and quadrato-jugal), such a contrast to the strong zygomatic arch in the horse where the food is ground, or in the tiger where the food is cut by the back teeth. The delicacy of the infra-temporal bar of the bird's skull is correlated with the fact that it has no very strong muscles attached to it and that it is not required to resist pressure. Since the maxilla is the chief tooth-bearing bone in reptiles and mammals, we cannot be surprised that it should be weakly developed in birds.

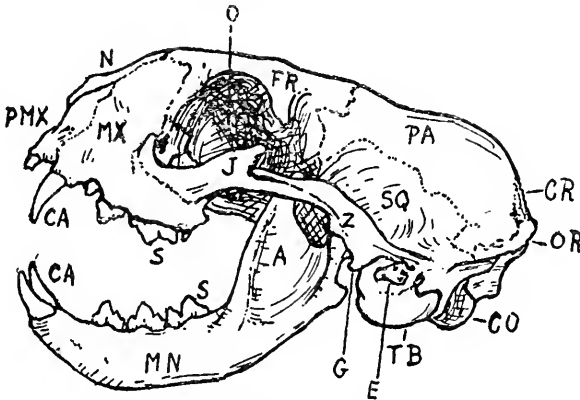


FIG. 15.—Cat's skull for comparison with bird's. C.O., one of the two occipital condyles; O.R., occipital crest for the insertion of muscles from neck and lower jaw; C.R., sagittal crest for the insertion of muscles from the lower jaw; P.A., parietal; F.R., frontal; O., orbit for eye; N., nasal; P.M.X., premaxilla (small); M.X., maxilla (large); J., jugal; Z., zygomatic arch, formed of the jugal and anterior process of the squamosal (S.Q.); G., post-glenoid process just behind the glenoid fossa of the squamosal in which the condyle of the lower jaw or mandible (M.N.) works; it prevents backward slipping of the lower jaw; E., ear-hole; A., ascending process of the lower jaw, to which strong muscles are attached; T.B., tympanic bulla protecting the drum or tympanum; S., sectorial or carnassial, a special cutting tooth; C.A., canine teeth.

(d) The importance of the eyes in birds is registered in the relatively large orbits with a thin vertical partition between them (the inter-orbital septum due mainly to presphenoid and mesethmoid), and with the large orbits may be correlated the restriction of the brain-containing portion of the skull to the posterior region which is very markedly broadened out. Thus the skull is built on a

different principle from that seen in types like skate and frog (platybasal), where the brain-case extends forwards between the eyes.

(e) The bird's skull has great freedom of movement on its single occipital condyle—a reptilian feature of course. It is usually very light for its size, the roofing bones having a markedly spongy texture. In this case, far from the lungs, the cavities of the bones are filled with air from the nasal and auditory passages.

We cannot leave the bird's skull without noticing two points of importance. Looked at broadly, as indicated above, it is a congeries of adaptations of a *general* nature. It may also show *special* adaptations, such as the broadening out of the bill in ducks or the elongation of the bill in some humming-birds. But these special adaptations concern superficial features, and in many cases they show their relative novelty by not becoming marked till some time after hatching. Quite apart from these superficial differences among birds' skulls are deeper non-utilitarian peculiarities, notably in the precise architecture of the palate. These are sure guides in the discovery of affinities; it seems that they have remained constant while more conspicuous adaptive features have been tacked on. In fact, there are deep architectural differences in the skulls which afford extraordinarily sure criteria of blood-relationship.

§ 5. ADAPTATIONS IN THE BACKBONE

The typical curvature of the articular surfaces of the bodies or centra of the vertebræ of birds is heterocœlous or saddle-shaped. It does not occur elsewhere. Looked at from in front, the centrum is concave from side to side and convex from above downwards. Looked at from behind, it is like a saddle. This typical shape is most marked in the cervical vertebræ, and its significance is in the freedom of movement it allows.

In rare cases other shapes occur, *e.g.* opisthocœlous (hollow behind) in the thoracic region of gulls and penguins.

In the extinct Cretaceous *Ichthyornis* the vertebræ were amphicæulous (hollow at both ends, like a double egg-cup), which is the shape characteristic of fishes. It occurs, however, in many extinct reptiles and in the extant geckos and the New Zealand "lizard," *Sphenodon*. It is rather interesting that the pro-cæulous type of vertebra (hollow in front), which is commonest in modern reptiles, never occurs in birds.

Several adaptations of the bird's backbone have been already noticed—the fusion of thoracic vertebræ in flying birds, to form a solid basis against which the wings can work; the complex coalesced syn-sacrum to which the ilia are fused over a long stretch, to facilitate the balancing of the body in bipedal progression; and the terminal fusion of caudal vertebræ in a plough-share which serves as a base for the tail feathers. It remains to notice that the neck is usually

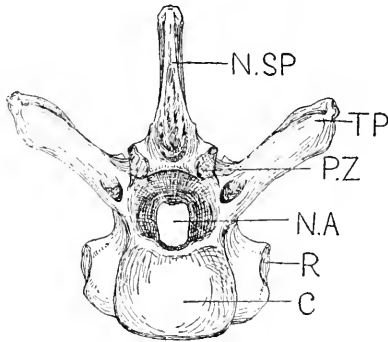
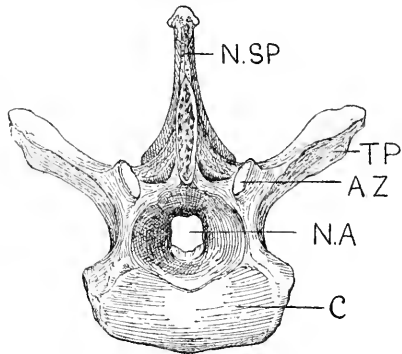


FIG. 16.—Dorsal vertebra of an ostrich. The upper one shows the anterior surface; the lower one the posterior surface. From a specimen. N.SP., neural spine; T.P., transverse process; A.Z., anterior articular process; N.A., neural arch, in shelter of which the spinal cord lies; C., the centrum or body; P.Z., posterior articular process; R., facet for the head of a rib.

very long, with a very variable number (8–24) of very mobile vertebræ, whereas mammals, with four exceptions, have seven. The neck of the bird must be long enough to reach the ground and to reach the preen-gland

which lies above the pygostyle. But the versatility is as striking as the relative length. A bird can move its head and neck through 180 degrees, so that the head rests between the shoulders with the tip of the bill pointing more or less backwards. The versatility is of great practical importance in catching rapidly moving booty. The neck-vertebræ often show well-developed cervical ribs, usually fused to the transverse processes, and serving for the insertion of numerous muscles. Some posterior cervical ribs may be free, but they never reach the breastbone.

The two-headed ribs, characteristic of the thoracic vertebræ, bear uncinæ processes (except in the Palæmediidæ), which overlap the rib behind and are bound to it by little ligaments. These processes are an inheritance from reptilian ancestors; they are well seen in that living fossil, *Sphenodon*. Their significance in birds is that they help to form the coherent sterno-costal-vertebral basket—important in connection with both flying and breathing. The upper or vertebral part of the rib, directed backwards, is connected at an angle to a bony (usually cartilaginous in mammals) sternal rib, which is directed forwards and articulates movably with the breastbone. When the angle, open forwards, between the vertebral part of the rib and the sternal part of the rib is lessened, and the distance between the thoracic vertebræ and the breastbone is thus likewise lessened, the air is driven out of the lungs (expiration). When the angle is increased and the breastbone sinks to a greater distance from the backbone, air enters passively into the lungs (inspiration). In birds, like divers, with very long ribs the difference in the volume of the body cavity as the angle between the vertebral ribs and sternal ribs increases or decreases is very notable, and has an obvious adaptive significance in relation to the prolonged immersion.

Behind the complex sacrum there are a number of free caudal vertebræ, terminating except in Running Birds in a pygostyle or ploughshare bone. This terminal fusion of vertebræ is also an adaptation, since it affords a basis for

the attachment of the rectrices or tail feathers. It is interesting to remember that no living bird has more than a very short tail as far as vertebræ go, the apparent long tails of pheasants and the like being, of course, made up of feathers only. On the other hand, the extinct Archæopteryx, the earliest bird known, had a long tail like a lizard's, with about twenty vertebræ.

§ 6. MUSCULAR SYSTEM

Birds show a high degree of muscular development. In some pigeons the pectoral muscles weigh half the whole bird. Every one who has picked the neck of a boiled fowl knows how many small muscles there are working this part of the body, a contrast to the scanty musculature of the stiff back-region. In birds that eat hard food the posterior part of the stomach has become a very muscular gizzard. Some of the adaptations of the muscles used in flight will be referred to later, but something may be said here in regard to perching. The toes are bent by perforati muscles which are inserted above the ankle-joint, but while these are contracted voluntarily, as may be watched in a bird of prey, there is also an automatic clinching. As the bird settles down on the tree the leg is bent at an angle; this stretches the tendons, and thus makes the toes grip the perch. In some birds there is a special perching muscle, the ambiens, inserted on the front of the pubis and continued down the anterior side of the femur. Its tendon, bending round the knee-joint to the opposite side of the tibio-tarsus, is inferiorly connected with the tendon of the flexor of the second or third toe, or with the third and fourth. It has nothing to do with the flexing of the first toe, and its importance has been exaggerated. The bending of the toes is mainly due to the active contraction of the perforati muscles already alluded to, and to the automatic stretching of the tendons as the legs are bent down.

When we consider the muscles of flight, of running, and of perching, the muscles working the rib-system and raising

the breastbone in respiration, the muscles of the gizzard if there is one, the two muscles running from the windpipe to the breastbone (sterno-tracheals), the muscles of the song-box, the muscles moving the eye and pulling down the third eyelid, the muscles of the heart, and so on, we see that the bird is a very muscular animal. But expert myologists tell us that the basis of the bird's muscularity is already laid down in the reptile.

Many people are familiar with the extremely hard tendons of some birds. In eating the leg muscles of game-birds the so-called "ossified" tendons which bind them to the bones are obtrusive. The hardness has been investigated by E. Retterer and A. Lelièvre (1911), who find that only a delicate zone has the characters of true bony tissue. The main mass of the hard tendon is due to hypertrophied tendinous tissue; the cells become very vesicular and the fibres are calcified.

CHAPTER IV

THE FLIGHT OF BIRDS

§ 1. Origin of Flight. § 2. Movements in Flight. § 3. Gliding Flight. § 4. Ordinary Flight. § 5. Sailing Flight. § 6. Velocity of Flight. § 7. General Biological Significance of Flight.

§ 1. ORIGIN OF FLIGHT

It is a reasonable hypothesis that birds ran before they flew, that they took flying jumps which sometimes landed them on trees, and that they practised parachuting for ages before they were able to do much in the way of true flight. Baron Nopcsa pictures a long-legged, long-tailed biped running along the ground and swinging its arms, which had acquired exaggerated scales—the beginnings of feathers—on their posterior margins. It is not inconsistent with this picture to suppose a subsequent arboreal apprenticeship, which is pointed to, for instance, by the gripping arrangements in the toes of birds—the tendons being kept from slipping by a roughened under-surface which catches on transverse ridges in the tendon sheath. The very primitive hoatzin climbs about when very young, using its clawed hands as well as its feet, and this may be a survival of ancient habit.

The flight of Pterodactyls depended on the possession of a patagium or fold of skin; so it is with bats; there is a little of this in front of the wing in birds, and there may have been more in ancestral forms, but everything depends on the feathers. These light, flexible, readily replaceable structures are, as we have seen, so closely coherent in their numerous component parts that they form an unsurpassed vane for striking the air. It is of great importance that

the sail-area can be increased by a lengthening of the feathers without necessarily involving much corresponding increase in the size of the bird. The character of the flight depends mainly on (*a*) the ratio of sail-area to size and weight of body, (*b*) the strength of the pectoral muscles, which often bulk largely in the total weight of the body, and (*c*) the shape of the wings.

In addition to the characters of the feathers, other primary adaptations are : (1) the shape of the bird's body which is well suited for reduction of resistance in passing quickly through the air ; and (2) the insertion of the wings high up on the thorax so that the centre of gravity is far below the centre of suspension, this being assisted by the ballasting of the aërial vessel, with the heavy organs below, *e.g.* pectoral muscles, heart, liver, and stomach, and with light organs above, *e.g.* lungs and air-sacs.

§ 2. MOVEMENTS IN FLIGHT

A physical account of the flight of birds is beyond our power and scope, but certain elementary considerations must be stated. The outstretched and upstretched wing which strikes the air is almost impermeable, partly because of the structure of the individual pinions and partly because the gaps between these are filled up by the wing-coverts. The under-surface is concave, both as regards the wing as a whole and each individual pinion.

In raising the wing for the next stroke, it is very important, as in rowing, that there should be economy of energy. This is effected by an automatic reduction of the size of the wing when it is not pressing against the air, by a movement of the individual feathers so that air passes between them, and by the convex upper surface which allows the air to glide off easily. Running across the quills of the pinions there is an elastic band which brings the feathers back into position again as the wing begins to descend. It is automatically tightened on the down-stroke, relaxed on the up-stroke.

The arched curvature of the under-surface of the wing is not to be thought of as like the interior of a dome. It is a subtle curvature, changing in different areas of the wing; and it differs considerably in different birds. Further inquiry will show that it is of fundamental importance in flight. It is largely because of the anterior arching of the anterior under-surface of the wing that the down-stroke makes the bird speed onwards, forcing the air out backwards.

It seems certain that the secondary feathers are of

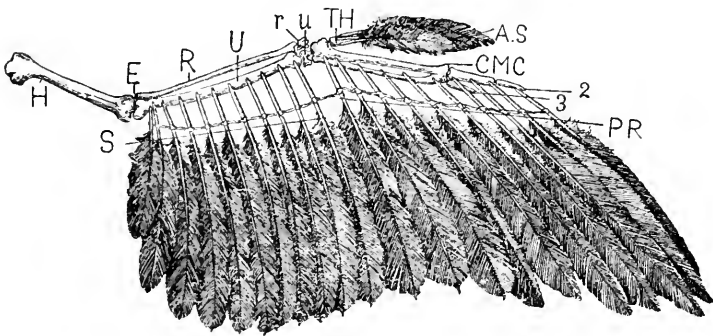


FIG. 17.—Wing of a bird, showing feathers and bones. From a specimen. H., humerus; E., elbow-joint; R., radius; U., ulna, r., radiale; u., ulnare; TH., thumb; A.S., ala spuria; CMC., carpometacarpus; 2, second digit; 3, third digit; PR., primary feathers; S., secondary feathers.

major importance in the stroke; it is by them that the air is most effectively gripped. The primary feathers are of great use for lateral steering, hence their exaggerated length in insect-catching swallows and swifts. They often project separately at their tips, so that the air passes between them, and it is pointed out by Hilzheimer that this allows the air-waves caused by the down-stroke to pass gradually outwards without producing a disadvantageous vortex.

Some steering is effected by the tail feathers, which also serve for balancing and as a brake or drag in flight. If the tail be spread out horizontally, the air driven backwards by the down-stroke of the wings strikes it from above and the bird rises—it may be avoiding a telegraph wire. If the

tail is cocked up the air driven backwards strikes it from below and the head region is depressed. It may also be that one side of the tail is spread horizontally while the other side is raised, so that the equilibrium of the body is preserved. A long neck, as in a heron, may function in the same way, and backward extended legs have doubtless their use. There may also be a vertical alteration of the flight by an active shunting of the shoulder-joint forwards, which would raise the head; or backwards, which would depress the head.

In his vivid "Animal Life," Professor F. W. Gamble points out that there are among animals four main modes of locomotion which may be compared to the alternatives open to a man in a boat provided with oars and a boathook. (1) He may punt with one of the oars pressed against the floor of the stream. The same sort of leverage, only more complicated, is seen in the walking of a beetle or of a man. (2) He may haul with the boathook fixed to brushwood or the low branches of a willow tree. So does the leech draw itself forward when it fixes its muscular mouth; so does the starfish pull itself up the rock with its many tube-feet. (3) He may scull from the stern of the boat with a single oar, displacing the water from side to side. So does the whale with its flukes or the fish with the posterior third of its very muscular body. (4) Finally, he may sit down and row with a pair of oars, as the insect called the water-boatman rows with its legs, or the turtle in the sea, or the penguin which swims with its wings as well as with its legs.

Now the ordinary flying is plainly of the *rowing* type of locomotion. The bird has in the down-stroke of the wings to push downwards and backwards a quantity of air heavier than its body—*heavier* since a short time has to be allowed for the up-stroke. The larger the wing the fewer strokes are required; the smaller the wing the more rapid the strokes must be. Hilzheimer gives the following figures for strokes per second: sparrow, 13; wild duck, 9; carrion-crow, 3-4; stork, 2; and pelican, $1\frac{1}{6}$. When the bird has got up a certain speed in the air the energy

required to go ahead on the same plane is much lessened. The question of resistance is discussed mathematically in the article "Flight" in Newton's "Dictionary of Birds," from which we take an illustration. A Rook, whose weight and wing-area were found by Sir George Cayley to be, roughly speaking, in the ratio of one pound to the square foot, would be able to glide horizontally whenever it had a velocity of 37.3 feet per second, which the bird can easily attain. The need for big pectoral muscles is more obvious when the bird is trying to launch itself from the ground into the air, or when it flies against the wind, or when it carries a heavy weight in its talons. The Great Northern Diver cannot rise from the land at all; the Cormorant is often seen taking a little run along the rock before it launches itself.

§ 3. GLIDING FLIGHT

The simplest mode of flight is that of gliding, when the bird having attained to a certain velocity rests on its oars for a while, or having attained a certain height descends to the ground without any stroke of its wings. A gull or a heron or any bird with a large sail-area, having got up a certain speed, glides along in the air without a wing-stroke; a pigeon launches itself from the dove-cot and glides to the ground; a hawk swoops from mid-air on its victim, and, missing it, glides up again without effort to a considerable height. The gliding flight can only be exhibited for a short time; the bird soon loses velocity or height. The time varies with the velocity previously attained or with the height from which the bird swoops down. Guidance during the gliding can be effected by spreading out the tail feathers, by raising one side of the tail and lowering the other, by moving the head and neck, or by partly flexing the wing on the side to which the bird wishes to turn. If we adopt the hypothesis that birds served an arboreal apprenticeship, it may be that gliding from branch to branch, or from the tree to the ground, was for a long time the main mode of flight.

During coasting flight, in gliding or in sailing, there is sometimes an interesting interlocking of the primary feathers, as Trowbridge (1906) demonstrated in hawks. He found that the edges of many of the primaries were

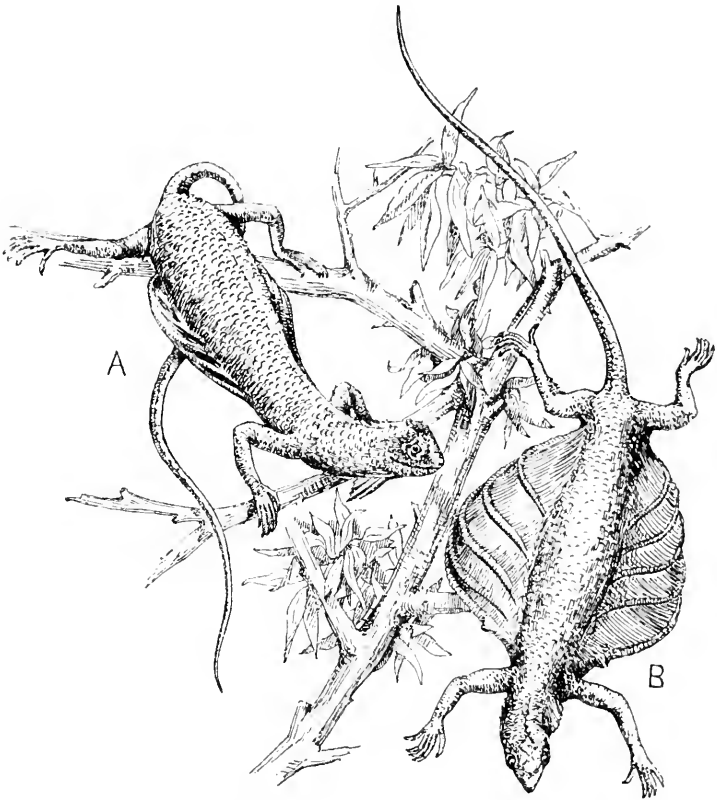


FIG. 18.—The so-called "Flying Dragons," *Draco volans*, parachuting arboreal lizards of the Far East. From a specimen. The skin is extended on about half-a-dozen elongated and movable ribs. As figure A. shows, the parachute is folded close to the side of the body when the animal is resting. Figure B. shows the parachute expanded as the animal leaps.

firmly interlocked. This makes the outer portion of the wing more rigid when the bird is using it as a vol-plane and it keeps the primaries partly extended without muscular exertion.

§ 4. ORDINARY FLIGHT

In ordinary flight the wings begin vertically above the bird's back, and the noise made when they strike together is very familiar in the case of pigeons. The wings move forwards, downwards, backwards, and then upwards again, the up-stroke taking place very quickly and costing the bird very little when it has got fairly a-going. The complete movement of the wing in ordinary flight is complex; the tip describes for each stroke a sort of figure 8 line, the lower loop of the 8 being much smaller than the upper.

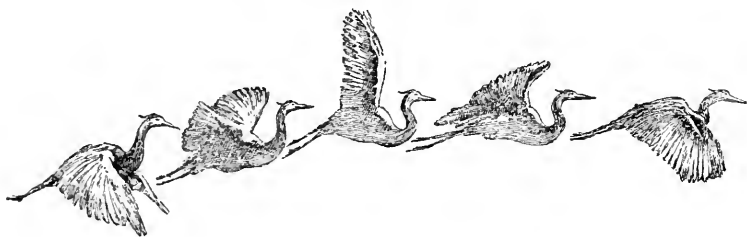


FIG. 19.—Flight of crested heron. After Marey. In the central bird the wings are vertically above the back. They come forwards, downwards, backwards (first bird to the left), and then up again.

Marey calculated that the energy expended by a pigeon when taking flight is five times as great as when it has acquired a certain velocity. Professor C. S. Roy wrote in the article "Flight" in Newton's "Dictionary of Birds": "The bird at starting makes rapid strokes with its wings, which move through a large angle—in the case of the pigeon striking one another above the back at the end of the up-stroke, and nearly touching with their tips at the end of the down-stroke. When velocity has been acquired, the flaps are slower, and the angle which they describe round the shoulder-joint is a very much smaller one. The reason why so much more energy is required to fly when they have little or no initial velocity relative to the air is due to the increased support afforded by the air if the wing-surface which strikes it be at the same time travelling

through the air in a line more or less parallel to its surface. The gain in resistance to the wing-stroke increases with the square of the velocity of the wing in a direction parallel with the axis of flight."

The steering laterally in ordinary flight is mainly due to differential action of the two wings ; rapid rising or falling to avoid an obstacle is mainly due to movements of the tail feathers and to slight displacements of the shoulder-joint forwards or backwards, the lower end of the coracoid moving in a deep groove in front of the sternum.

§ 5. SAILING FLIGHT

The most remarkable mode of flight is that called "sailing," so well illustrated by albatross and vulture. It is characterised by prolonged circling without active strokes of the wings, yet without more than temporary loss of velocity or altitude. The albatross describes magnificent ellipses round and round the ship, apparently without effort, apparently without a stroke of its wings for half an hour at a time. It cannot be said that sailing flight is more than partially understood. The following statements may be ventured upon :—

(1) Sailing flight is characteristic of birds that have a large sail-area in proportion to total weight, such as albatross, vulture, stork, and crow.

(2) Sailing flight is not exhibited unless there is some breeze, and of course there may be considerable currents overhead when it is relatively still on the ground. But there can be no sailing in a dead calm.

(3) There are no visible strokes of the wings, but there is a frequent change in the tilt of the body which may be referred to movements of tail feathers, shoulder-joint, neck, and head. There is wheeling as well as tilting when the bird turns in its course and proceeds in the opposite direction ; for it is certain that the sailing bird flies alternately with the wind and against the wind. Besides movements of parts of the body in relation to one another, there

is some internal work in keeping the wings outstretched and taut.

(4) In going down the wind the bird sinks a little ; in going up into the wind it rises again, and it may rise higher than it was before. Moreover, the albatross not only circles round the ship but it keeps pace with it. In all probability the energy of locomotion acquired by increased velocity when sailing with the wind is changed into energy of position as it rises with reduced velocity against the wind.

(5) The theory that the bird takes advantage of strong upward currents may probably be ruled out, since it does not readily account for horizontal progress and since sailing has been clearly demonstrated while light objects like feathers sank slowly in the air. But our knowledge of the currents in the air is still very young.

When a gull flying against the wind from the fields shorewards comes just above the edge of the cliffs, it often meets a strong upward current, caused by the cliff diverting the breeze from the sea. In such a case the gull often rests on its oars ; it not only rises, but continues its previous course without further strokes of its wings. But this gliding continues for a very limited time and it is not comparable to true sailing ; the gull is taking advantage of a considerable velocity attained by previous strokes of the wings and of the strong upward current off the cliffs.

(6) A widely accepted view, supported by Lord Rayleigh and others, is that the sailing bird takes advantage of the unequal velocity of the air at different heights. In its sinking as it sails with the wind the bird will be meeting currents which are more and more retarded by proximity to the surface of the earth. If at the lowest level of its trajectory the bird tilts its body and rises facing the wind, it will meet successive currents of air which are less and less retarded by proximity to the earth ; the air-resistance, which is the lifting force, will be greater than if the air were in uniform movement at all levels. An argument in favour of this theory is that the sailing birds, though moving in great circles or ellipses on the whole horizontal, are seen to

ascend and descend a little in regular alternation. An argument against the theory may be found in the fact that vultures circle and circle, hour after hour, at great heights where the inequality of the velocity of currents will be less marked than in closer proximity to the earth.

(7) It is possible that very slight strokes occur, such as an oarsman, having attained a great speed, might give with the tips of his oars. For it seems hazardous to dogmatise as to what may be happening in the case of vultures at an immense height. The telescope shows that there are no visible strokes in the ordinary sense, but a very little might go a long way. In sailing birds the tips of the primaries project separately from one another, and their tilt is subject to continual alteration. Again, it must be remembered that the under-surface of the bird's wing is not like the inside of a dish-cover; it is a very complex curved surface, and it is not rigid. The possibility of very minute strokes and of alterations in the curvature of the under-surface of the wing will be rejected by most ornithologists. But we would point out that it is not inconsistent with the fact that, at certain parts of their wheeling, vultures have been seen putting on a brake as if they were going too fast. There may be velocity to spare one minute, and not more than enough the next.

(8) Another possibility not to be left out of account is that vortex movements of the air, which may be partly due to the bird itself, may play a part in sustaining what comes so near the modern "glider."

§ 6. VELOCITY OF FLIGHT

The frictional resistance which slows the movement of a ship through the water has a very slight influence on the bird in flight, and when the bird has got thoroughly going the tendency to sink is counteracted by the horizontal velocity. As Professor Roy notes: "Of the greatest importance for the flight of birds is the fact that the resistance offered to the motion of a flat body in a direction at right

angles to the plane of its surface is very greatly increased if it be made to move at the same time through the air rapidly in a direction parallel with its surface." The supporting force, which is the thrust upwards on the bird's wings and body, increases with the square of the velocity, and varies also with the surface of the bird and with the density of the air. The precise formula is given in Professor Roy's article in Newton's "Dictionary of Birds."

It seems safe to say that some common birds, like the starling, readily attain for a short time to a velocity of over 40 miles an hour. A carrier pigeon can keep up 40 miles an hour for a considerable time, but this will be halved against the wind and nearly doubled with the wind in the bird's favour. Hilzheimer cites the case of a swallow which flew along with carrier-pigeons from Compiègne to Antwerp, a distance of about 140 miles. It accomplished this in 1 hour 8 minutes, reaching its nest a long time before the first pigeon. This is a well-known case, often cited, but von Lucanus (1921) points out that it is not above criticism. It seems very doubtful if sufficient care was taken in the marking of the swallow ("un peu de couleur") and in making quite sure that the swallow seen entering the nest at Antwerp was the identical swallow that left Compiègne a little over an hour before.

§ 7. GENERAL BIOLOGICAL SIGNIFICANCE OF FLIGHT

The Vertebrate transition from water to dry land was made by Amphibians. From some Amphibian stock there probably evolved the race of Reptiles, partly terrestrial, partly aquatic, and, in the case of Pterodactyls, aerial. From a bipedal terrestrial race of Reptiles, probably the Dinosaurian Ornithischia, arose the Birds.

The problem of true flight has been solved four times—by Insects, Pterodactyls, Birds, and Bats—and the four solutions are very different. In insects the lightly built body, containing a good deal of air in the much branched tracheæ, is sustained and propelled by the extremely rapid

vibration of the wings, far more rapid in most cases than anything seen among birds. Thus a bee vibrates its wings more than 200 times in a second, and for a short distance the bee can outfly the pigeon.

In Pterodactyls an extension of the skin was borne out on the extremely elongated outermost finger, usually counted as the little finger. The power of flight was probably not very great, for the keel on the breastbone, to which the muscles working the wings would be attached, is at most slight.

In bats a double fold of skin, beginning at the sides of

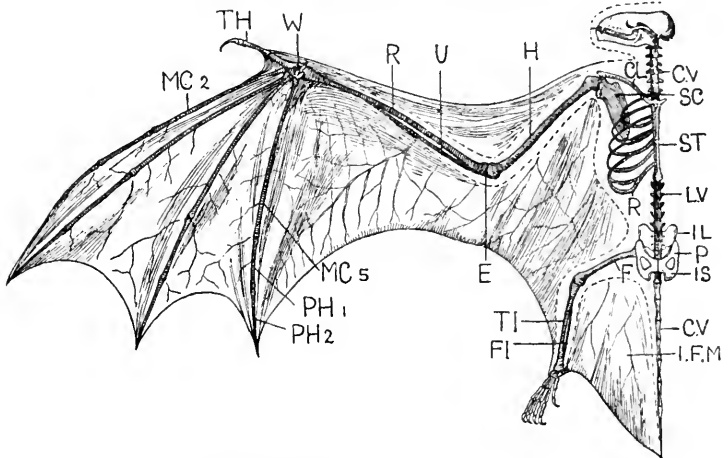


FIG. 20.—Bat's wing and skeleton. From a specimen. H., humerus; U., splint-like ulna; R., radius; W., wrist; TH., thumb; MC.2, second metacarpal or palm bone; MC.5, fifth metacarpal; PH.1 and PH.2, its two phalanges or finger-joints; E., elbow; TI., tibia; FI., splint-like fibula; F., femur; I.F.M., inter-femoral membrane; C.V., caudal vertebrae; C.V., just below the skull refers to cervical vertebrae; CL., clavicle; SC., scapula; ST., sternum; R., ribs; L.V., lumbar vertebrae or loins; IL., ilium; P., pubis; IS., ischium.

the neck, is stretched out along the anterior margin of the arm, and, skipping the thumb, is continued between the greatly elongated metacarpals and phalanges to form the wing proper. This tapers off, however, down the side of the body to the hind leg, and between the hind legs to each side of the tail (forming the inter-femoral membrane) if there is a tail.

These four types of wing are analogous, for all of them are used in actively striking the air. But the wings of insects, which originate as hollow outgrowths from the dorso-lateral regions of the two posterior segments of the thorax (mesothorax and metathorax), are not in any way comparable, as regards development or structure, to the wings of Pterodactyl, Bird, and Bat which are transformed fore-limbs (and rather more in Bats). This is expressed by saying that the wings of insects are analogous but not homologous with the other wings. On the other hand, if

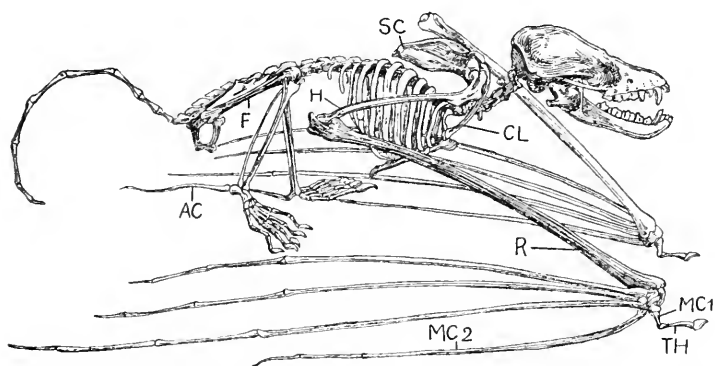


FIG. 21.—Skeleton of bat, creeping. sc., scapula or shoulder-blade ; cl., clavicle or collar bone ; h., humerus or upper arm ; r., radius of forearm ; mc.1, metacarpal of the thumb (th.) ; mc.2, metacarpal or palm bone of second digit ; f., femur, or thigh bone ; ac., special heel bone.

we keep to the main part of a bat's wing, we may say that the wings of Pterodactyl, bird, and bat are both homologous and analogous with one another, being transformed fore-limbs and organs of true flight. If we compare any of them with our own fore-limb, we see a general similarity in structure and mode of development, but there is no analogy.

These distinctions, first made clear by Sir Richard Owen, are not mere pedantries, but enter deeply into the interpretation of organic structure. Let us take Sir Richard Owen's examples :—

(1) The Wing of a Bird and the Arm of a Man—Homologous but not Analogous.

(2) The Wing of a Bird and the Wing of a Butterfly—Analogous but not Homologous.

(3) The Wing of a Bird and the Wing of a Bat—Homologous and Analogous.

The transition from water to dry land, whether prompted by necessity or the spirit of adventure, or by both, made for progress, but it was attended in the first instance by obvious disabilities.

(1) The supply of oxygen was more copious but it was more difficult to tap, especially when the skin of the immigrants on to the land had to be protectively hardened. Every one knows that the solution arrived at was having internal surfaces—notably the lungs of Amphibians, Reptiles, Birds, and Mammals. The branching air-tubes of insects, taking air to every hole and corner of the body, illustrate another idea.

(2) In water there is great freedom of movement, up and down, to right and left, forward or backward, in many planes. But the transition to dry land implied restriction to one plane—the surface of the earth. This involved great risks and led no doubt to improved musculature and to better brains for controlling the necessarily precise movements. We can understand why many terrestrial animals have added to their possibilities of movement by becoming burrowers on the one hand and arboreal on the other. But flight is a fine illustration of the way in which a disability leads to a new advance. The cat's discomfiture as the stalked sparrow flicks into the air is a familiar illustration of the survival value of flight.

(3) Another disability attendant on the possession of the dry land concerns the eggs and the young. Aquatic animals can shed their eggs or liberate their young with much more security than is possible for terrestrial animals. For the water is present as a universal cradle, supporting and washing the delicate young lives. But to lay eggs or to liberate young ones on the dry ground is often to

court disaster—they will be dried up or devoured or blown away. Now there are many ways of circumventing this difficulty ; there may be hard protective shells ; there may be a burying of the eggs ; there may be a carrying of the eggs by the parent ; there may be a secondary return to the water, as in many insects ; there may be a carrying of the young for a long time before birth and the bringing forth of the young at a relatively advanced stage ; and there may be a carrying of the young after birth as in marsupials and bats. But flight opened up a new possibility—to have a nest in a safe place among the branches or in the crevices of the rocks.

It is plain that the power of flight justified itself in the struggle for existence in a great many different ways. It gave its possessors a new safety and independence ; it enabled them to follow their food and to seek for water over long distances ; it enabled them to secure the well-being of their offspring by building nests in well-concealed places, often inaccessible except to enemies who could also fly. More than that, the power of flight in its high development gave birds a unique power of annihilating distance, of evading the winter, of having two summers in the year, of having two homes, of changing their season in a night. In seeking out suitable feeding-places and breeding-places neither space nor time presents to the flying bird any obstacle.

We cannot pass from flight without at least a recognition of its individuality. There are many different modes, each with its quality—some quiet and others bustling, some apparently slow and others apparently in haste—some silent and others noisy. The owl flits from tree to tree without a hint of a sound, and the usefulness of this is obvious. The Manx Shearwaters (*Puffinus anglorum*) sleep in their burrows by day, and start out on their labours at dusk. In the silence of their flight they compare well with owls. Dr. F. M. Ogilvie writes : “ They have a curiously silent flight, gliding past one in the gathering gloom like ghosts indeed. I know no bird, except perhaps

some of the owls, whose flight is so absolutely noiseless. The effect is curiously uncanny ; they appear suddenly out of the darkness and disappear again like spirits of another world."

Some other modes of locomotion among birds are referred to in connection with haunts—the swift running on the desert, the hopping from branch to branch, the ouzel's "flying under water," and how many more. In many cases we recognise the same touch of perfection that we see in flight. Thus the instantaneousness of the disappearance of some of the diving birds is like magic, we cannot see how the trick is done. Dr. F. M. Ogilvie (1920) gives a fine description of a familiar sight : "The Shag's—and, indeed, all the Cormorants'—method of diving is absolutely characteristic. He really springs right out of the water, turns over in the air, and takes a noiseless header ; but the body is so close to the water throughout the manœuvre, and the action is so quick, easy, and free of effort, that one hardly follows the middle stage where the body of the bird is really out of the water altogether, the moment when his paddles are just leaving the water with his kick off, and the beak is just meeting the water to complete the downward half of the semicircle which he describes."

CHAPTER V

FOOD : ITS CAPTURE AND UTILISATION

§ 1. Methods of Food-getting. § 2. Adaptations of Bills, Tongue, and Feet. § 3. The Food-canal and its Annexes. § 4. Physiological Summary.

THERE are, after all, only two fundamental vital "urges"—"hunger" and "love"; but both terms must be thought of "in inverted commas," for they include all the ways of caring for self and all the ways of caring for others. As the poet said long ago: "Why do the people so strive and cry? They will have food, and they will have children, and they will bring them up as well as they can." So it is with animals. "Hunger" and "love" are the *motifs* of the drama of life.

§ 1. METHODS OF FOOD-GETTING

There is a wide range of diet among birds and much individuality in the methods of food-getting.

I. Vegetarian.—Many birds eat fruits and seeds, and some devour buds and leaves. Among the bud-destroyers there are some, like tits, that are really seeking for small insects in the vicinity. Some woodpeckers make holes in a tree and tap the sugary sap; humming-birds suck up the nectar of flowers. The ptarmigan on the hills often eat lichens.

II. Carnivorous.—Birds play an important part in keeping a check on small mammals, such as mice and voles. The kestrel is a good example. Others, like the sparrowhawk and peregrine falcon, the owls and the carrion-crow,

depend to some extent on other birds. The golden eagle accounts for a good many grouse, and probably serves as a useful eliminator, keeping up the standard of racial fitness. Not a few birds, such as crows, steal the eggs of other birds. Mr. Beebe relates that a South African raven breaks ostrich eggs and an Australian Black-breasted Buzzard breaks emeu eggs by letting a stone fall on them. The Secretary Bird's bill of fare includes snakes and our rooks allow fresh-water mussels to fall from a height so that the shells are broken. The ranks of frogs are thinned by storks, and of fish-eaters there is a long and varied list from the flightless penguins to the albatross, from the hovering osprey catching the trout in its talons to the diving cormorants, from the patient heron to the restless Frigate-bird in the open sea.

Cuttlefishes are captured by penguins; the oystercatcher is skilful in opening mussels; rooks take clams and sea-urchins to a height and let them drop on the stones; all sorts of shore animals are eaten by birds. The thrush breaks the shells of the wood-snails on its stone anvil, and the Pied Wagtail is fond of the little fresh-water snail, *Limnaea truncatula*, which harbours the young stages of the liver-fluke.

One of the most important facts in regard to birds is that they check the tendency that many insects have to over-multiplication—a tendency which is a continual menace to the balance of nature. Mr. Beebe writes: "It has been said that without birds, within a space of ten years, the earth would not be habitable for man, owing to the unrestricted increase of noxious insects. There is doubtless not a single group of insects which does not suffer from the appetite of one or more species of bird." The cuckoo is partial to hairy caterpillars; the swallow and the swift hawk insects, usually small, in mid-air; the goatsuckers with their big gape work by night and the flycatchers with their sharp eyes work by day; the hen scratches up the eggs and larvæ hidden in the ground and some of the woodpeckers gouge grubs out of holes in the

PLATE III



COMMON HERON (*Ardea cinerea*).
Fishing by the lake-side in the evening.

trees. One may almost say that there is no end to the diversity of ways in which birds deal with insects.

III. Mixed Feeders.—Many birds enjoy both vegetarian and carnivorous diet. The thrush has its fruit and its snails ; ducks eat a lot of duck-weed but they are ready for all sorts of small aquatic creatures ; the Carrion-Hawks of South America devour carrion, sickly lambs, the snakes roasted in a veldt fire, and vegetable food. The last is an extreme case, but it must be said of many birds that they are not fastidious. Often they will feed on insects during one season and on vegetable materials during another. Of special interest are those cases where the young are fed on a kind of food different from that on which the adults mainly depend. Thus the young rooks are fed for a while on insects only and the same is true of young sparrows.

IV. Oddities of Diet.—The Kea Parrot (*Nestor notabilis*) of New Zealand, though belonging to a race habitually vegetarian or frugivorous, has taken to killing sheep, and does very serious damage in certain places. It alights on the sheep above the loins, tears aside the fleece, and cuts open the skin with its strong bill, and devours the fat and flesh near the kidneys. To account for this remarkable change of habit, it has been suggested that the bird began by pecking at the fat adherent to the sheep-skins hung up to dry. It is said to enjoy its mutton-chop at the Zoo.

These changes of diet are of much interest both theoretically and practically. They illustrate variations in habit, tentative answers-back in the struggle for existence. The herring-gull is normally a fish-eater, but in the last quarter of a century in the North of Scotland it has become increasingly vegetarian, frequenting the farmer's fields and devouring turnips, potatoes, and the ears of corn from the stooks. During the summer the Black-headed Gull is very largely insectivorous, and Mr. Beebe notes that on the pampas near Buenos Ayres the people look for the flocks of gulls as the only relief from the hordes of grasshoppers. A woodpecker, as Selous notes, may occasionally function as an ant-eater.

The Red-winged Starlings of South Africa include in their menu the berries of the syringa, which they eat in such quantities that they are stupefied by some included narcotic. Similar states of intoxication have been observed in woodpeckers, who tap the stems of the sugar-maple and in some frugivorous birds who indulge in fermenting fruit. One would like to know more about the hairs of the hairy caterpillars for which cuckoos have so strong an appetite. They accumulate, as is well known, in the stomach, and the rhythmical movements continued during the churning and digestion press them against particular areas of the mucous lining of the stomach and embed them firmly. Are they shed after a time? Are they thrown up as pellets? Are they helps or hindrances to digestion? Further inquiry is necessary.

Detection of Food.—In most cases the food is seen and the acuteness of the bird's vision is well illustrated by the success with which gulls pick up fragments of biscuit in the white wake of the steamer. Touch plays an important part in birds which feel in the mud for small animals; thus the snipe's elastic bill is richly innervated. Of smell there is not much evidence except in nocturnal birds of prey, to which blackbird, magpie, rook, and a few more may be added. Longfellow was probably right when he indicated in *Hiawatha* that it is by sight, not by smell, that the vultures gather to the carcass—

“ Never stoops the soaring vulture
 On his quarry in the desert,
 On the sick or wounded bison,
 But another vulture, watching
 From his high aerial look-out,
 Sees the downward plunge and follows ;
 And a third pursues the second,
 Coming from the invisible ether,
 First a speck, and then a vulture,
 Till the air is dark with pinions.

So disasters come not singly . . .”

Modes of Food-Capture.—An endless succession of pictures passes through the mind : the swift rushing through

the air after flies and gnats, the kiwi running about at night probing for earthworms and looking out for a big phosphorescent one, a woodpecker making a hole in a tree and another using its sticky tongue to lick ants into its mouth, the oyster-catcher knocking a limpet off the rock with a dexterous stroke of its strong bill, a duck systematically exhausting the mud in a corner of the pond, a heron standing like a statue and suddenly relaxing as the trout flicks past, a solan-geese diving from a height, a creeper running up the tree like a mouse, a kestrel hovering in mid-air and coming down like a bolt—a bolt from the blue for the field-vole. The shrike has not strong feet for holding its booty, it spikes the small mammal or bird, or the large insect, on thorns near its nest; the nut-hatch, chiefly insectivorous, fixes nuts in crevices and cracks them; the thrush breaks snail-shells on its anvil; the skua-gull forces other gulls to disgorge the fish they have caught; the Greek eagle drops the tortoise from its talons from a great height.

The snipe's longish bill enables it to probe for small creatures, such as worms, in the mud, and the far back position of the orbits may be adaptive. Dr. F. M. Ogilvie writes: "A snipe, with its eyes placed as they are, can get the very last fraction out of its bill, as it struggles for a worm half an inch further down in the mud, and yet see all that is going on round it, and be ready for any emergency that the fates have in store." The delicate skin prolonged over the bill is rich in nerve-endings with a tactile function. The same is true in the woodcock, which depends very largely on earthworms, and has a very sensitive bill. There is in this case a further adaptation that the tip of the bill is slightly movable by itself and may facilitate the hooking up of the earthworm.

A peculiarity exhibited by gannets and some other birds is storing food. Gannets frequently fly 50 miles to their fishing-ground, but in spite of the labour thus involved they often collect far more food than they need, a fact unpleasantly conspicuous in the stench of the colony. Dr.

F. M. Ogilvie (1921) suggested that the explanation of this storing instinct is to be found in the fact that gannets feed on surface-swimming fish and are therefore dependent for their food supply on the weather. When it is stormy the fish swim at a greater depth. "If the gale continues for three or four days, during the whole of that time the bird will catch nothing, and it is possible that the fear of such a catastrophe occurring is at the root of the habit, and that the bird's instinct teaches him always to keep a day or two's supplies in hand, as long as he is able to do so." Perhaps, since we do not know much about a bird's foresight or fear, it would be safer to say that the frequently recurring vicissitude of storm has served to sift out variations in the direction of a storing instinct.

§ 2. ADAPTATIONS OF BILLS, TONGUE, AND FEET

The absence of teeth in modern birds is compensated for, as in tortoises and turtles, by the development of the horny bill covering the jaws. It has often a sharp edge suited for cutting and tearing, and it goes beyond the function of teeth in its adaptations to capturing the prey. There is not much real chewing or mastication in birds, but parrots gnaw their nuts, and a captive golden eagle will with very rapid movements of its beak dislocate the vertebræ of a trout from end to end. It might be convenient to keep the word "bill" for the horny sheath and the word "beak" for bill and jaws combined.

A generalised bill may be illustrated by that of the crow and allied birds—strong, pointed, somewhat triangular in section, suited for many different purposes. Shortening, sharpening, and curving such a bill results in the effective instrument of the bird of prey; it is quick to kill by piercing the skull or breaking the neck or cutting the jugular vein, it is also well suited for the rapid skinning or plucking of the victim. On the same line of evolution are the bills of the carnivorous owls and the vegetarian parrots, a peculiarity in the latter being the movable hinging of the premaxillæ

to the front of the rest of the skull. Parrots often gnaw into hard nuts or grind hard seeds to powder, there being file-like roughnesses to the inside of the bill.

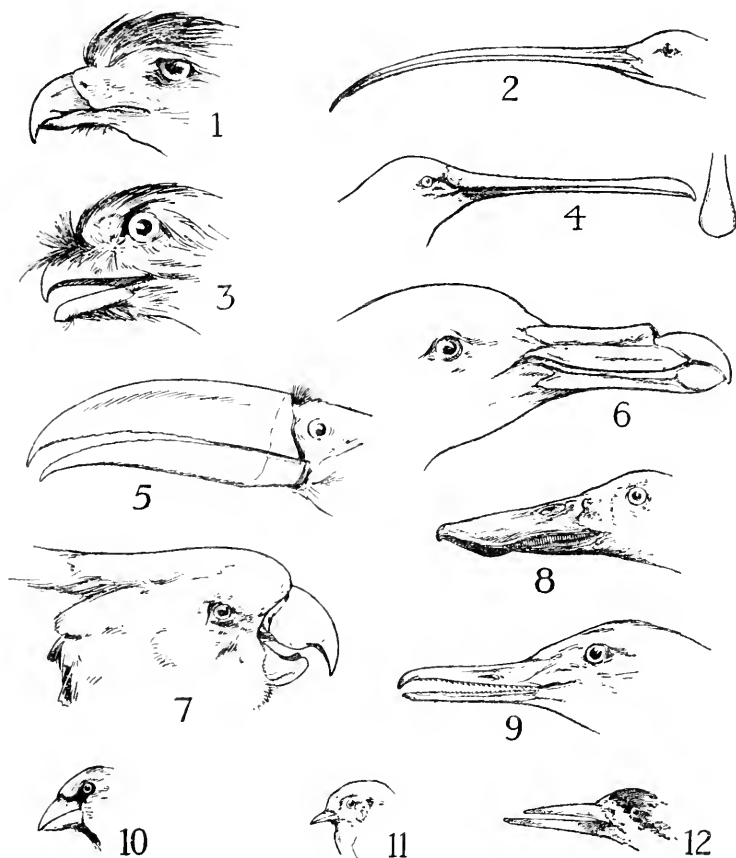


FIG. 22.—Types of beak. 1, eagle (hooked); 2, curlew (decurved); 3, goatsucker (wide gape); 4, spoonbill (spatulate); 5, toucan; 6, giant petrel; 7, cockatoo; 8, spatula duck (lamellate); 9, goosander (serrate); 10, hawfinch; 11, robin; 12, rhyncops or skimmer.

Adaptations for fish-catching by spearing are seen in the snake-bird; by gripping in gannet, cormorant, and merganser; by engulfing in the pelican. The puffin

catches small fishes in its laterally compressed "coultter-like" bill, and is able to add one after another till it has perhaps five, the tongue being probably used to hold the captives firm when the beak is opened to add others. Extreme specialisation is seen in the Skimmer (*Rhyncops*), a sort of tropical tern, where the bill is long, high, and as thin as a paper-knife. The bird flies very close to the surface and skims the water with the mandible which is longer than the upper jaw. When the knife-edge of the mandible touches a little fish or a shrimp it projects the booty into the open mouth. The skimmer is also said to skim the soft mud. The very opposite extreme is seen in the broad bills of ducks and geese, which are used in sifting small animals out of the mud. The sifting is facilitated by horny fringes on the bill and also on the tongue. In the Shoveller Duck the arched bill has comb-like epidermic processes at the edges which form an effective sieve for keeping the food in while the water drains out. In the related long-legged Flamingo the lower jaw is much arched and the whole beak is bent down on itself, almost at right angles, so that it is thrust upside down into the mud from which it sifts out small molluscs and the like.

Another line of evolution is illustrated by the long slender bills of some of the humming-birds which are well suited for probing to the nectar hidden deeply in the flowers, and also in some cases for extracting a small insect from a crevice. The opposite extreme is seen in the broad, widely gaping, short bill of the swifts and the goatsuckers, very well suited for capturing insects in mid-air. Similarly, we may contrast the slender bills of wrens and warblers, suited for dealing with small insects, and the thick conical beaks of finches suited for opening dry fruits and cracking dry seeds.

From a few we may learn all, and it is not necessary to go further in illustrating the adaptations of bills. Three points, however, should be noted.

(1) The adaptations often show a remarkable nicety, which indicates the specialised mode of feeding in many

birds. In the struggle for existence there has been a utilisation of all manner of openings or vital niches, and thus the direct competition of related species has often been avoided. The mandibles of the crossbill (*Loxia*) cross one another at the tips, and form an instrument very effective in extracting the seeds from the fir-cones. In the Wry-bill Plover of New Zealand the bill is bent to one side, as the Oyster-catcher's sometimes comes to be, and that is suited for capturing insects and other small fry from beneath loose stones. Professor Newton describes the dimorphic bills of the Huia birds of New Zealand: the short-billed male chisels holes in decaying wood; the long-billed female probes the crevices in harder wood; but when he, having discovered a grub in his excavations, is unable to reach it, she comes to his aid.

(2) It is interesting to note that the most striking features of a specialised bill are not put on until the young bird begins to fend for itself. The curlew has a very long bill in proportion to its body, but there is very little indication of this within the egg. The very young flamingo shows nothing of the characteristic deflection of the bill, and it is not till the young skimmer joins its parents on the sea that the lower jaw grows out far ahead of the upper. We see then that the inheritance of the organism is more fully expressed when new liberating stimuli begin to operate.

(3) Another point of general biological interest is that similar bills may occur in birds that are not nearly related to one another, *e.g.* in birds of prey and parrots, in swifts and swallows, in spoonbill and spoonbill-plover. This illustrates what is called "convergence." From different sources similar adaptations have been evolved in relation to similar conditions of life. It is plain that a plastic superficial feature is not of much use in working out a "natural classification." On the contrary, it is apt to lead one astray. One must base conclusions as to affinities or blood-relationship on deeper features, such as differences of architectural plan in the skull.

Adaptations of the Tongue.—In many cases the

tongue bears soft or horny processes which help to guide the food backwards to the gullet, or guard the opening of the glottis, or help in ducks to strain the mud. In some fish-eating birds, like pelicans and kingfishers, which swallow their prey whole, the tongue is very small ; it is better out of the way. In the insectivorous woodpeckers it is very long, and the branches of the hyoid bone to which its muscles are attached come forwards over the top of the head as far as the nostril, forming a kind of spring which makes the retraction of the sticky tongue exceedingly rapid. In the sap-sucking woodpeckers the tongue is comparatively short and has a tip like a brush. The same brush-like termination is seen in lorries, and the tongue of the humming bird ends in two delicate brushes, suited for nectar-sucking and capturing small insects. Cockatoos have a fleshy tongue, ending in a club-like knob ; in many birds, like larks, the tongue is bifid as in snakes and some lizards. The tongue may have spines on it as in insect-eating woodpeckers, or prongs as in the chickadee, or fleshy papillæ as in the flamingo, and so on almost endlessly.

One should not leave the tongue of birds without recalling the fact that this structure made its first appearance in fishes, but in a non-muscular form. Fishes cannot move their tongue, if they have one at all. Even in the young tadpole of the frog the tongue is still non-mobile ; there are muscle-fibres in it, but they are not strong enough at first to move it. Perhaps their first use is to compress certain glands in the tongue. But they grow in strength, and the adult frog, as every one knows, has a very mobile tongue. The tongue becomes the fine touch-organ of snakes, the very long clubbed insect-catcher of chamæleons, the long, sticky, worm-like ant-catcher of the ant-eater, the mouth-hand (we may almost call it), with which the grazing cattle grip the grass, and some illustration has been given of its varieties of form and use in birds. We see, then, how a structure which in its earliest appearance seems to be devoid of much significance is gradually improved upon and reaches perfection along many different lines.

Adaptations of the Feet.—Most of the special adaptations of birds' feet have, of course, to do with walking, running, hopping, climbing, swimming, and perching, but

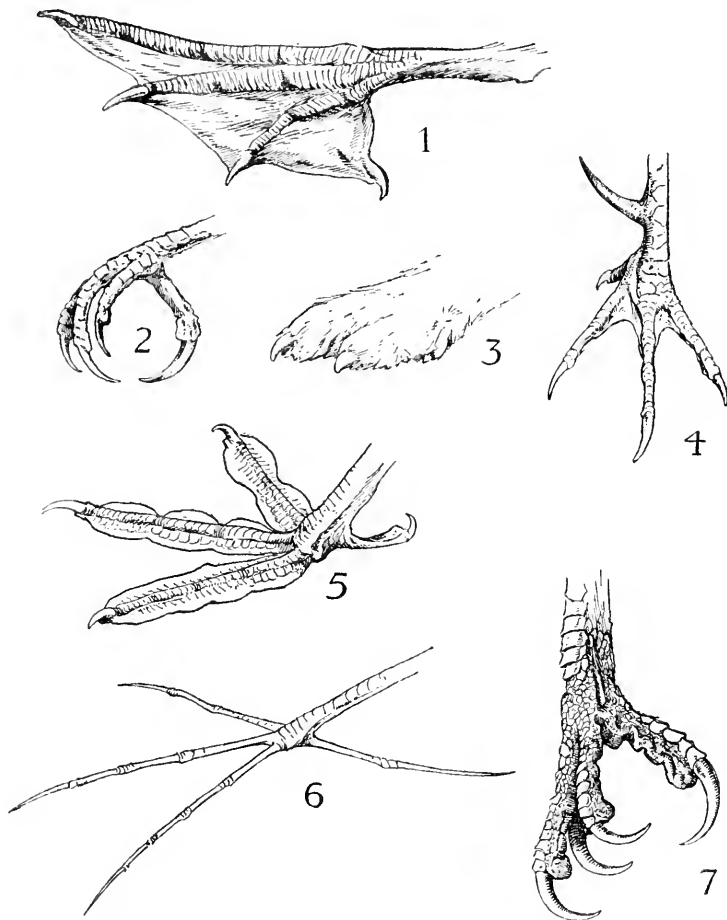


FIG. 23.—Various types of feet in birds. 1, shag (swimming); 2, crow (perching, lifting); 3, ptarmigan (stockinged in feathers); 4, jungle fowl (walking, scraping); 5, coot (lobate, swimming); 6, jacana (suited for walking on floating plants); 7, sea-eagle (raptorial).

some have to do with food-catching. The parrot uses its foot as a hand, picking up its food and holding it to the

mouth; the jacanas or gallinules which have very long toes, suited for walking on the floating leaves of water-lilies, lift aquatic plants to their bill and pick off the small animals; the fowl-like birds use their strong blunt claws to scratch the ground and the wood-storks stir up the mud in the shallow pools with their toes; the secretary bird, a kind of terrestrial vulture, strikes the snake with its foot and sometimes kills with one forward kick; the owls can bend their fourth toe backwards beside the first toe, and this forms an effective instrument for catching, crushing, and carrying a mouse; the osprey has a similar trap for fishes, and their slipperiness is met by sharp hard pads below the toes. The eagle's foot with the first toe backward and the others forward, worked by powerful muscles and tendons, and armed with sharp strong claws, is unsurpassable. The golden eagle on the moor seizes the grouse among the heather without stopping in its flight, and carries it in its talons to its eyrie. There it holds the dead bird with one foot, while it plucks off the feathers and tears up the flesh with its bill. Mr. Beebe notes that in vultures which feed upon carrion the toes have lost their clasping power.

§ 3. THE FOOD-CANAL AND ITS ANNEXES

The mouth cavity is lubricated by the secretion of the salivary glands, which differ greatly in their degree of development. They are large in birds like woodpeckers, in which the tongue is covered with viscid secretion, useful as a glue in insect-capture. They are peculiarly large in the sea-swift, *Collocalia*, where the salivary secretion, largely consisting of mucin, is used to make the nest. The digestive function of the salivary juice (turning starch into sugar) does not seem to be very important in birds, which are so much given to "bolting" their food, but no doubt some of the secretion will accompany the food into the gullet and into the crop if there is one.

The muscular region at the back of the mouth is the pharynx, and its function is to grip the food in the process

of swallowing. It is from this region in the embryo that the gill-clefts grow out and the thyroid gland arises as a median ventral diverticulum. The gill-clefts are transitory structures, mere relics of distant ancestry, except the first one, which persists as the Eustachian tube from the ear passage to the back of the mouth.

The gullet or œsophagus is an elastic tube, with mucus glands lubricating it internally. It may serve to store food, as in cormorants, without there being any special crop. Every grade may be found between a narrow gullet and a capacious one, between the presence of a huge crop and its entire absence.

The crop is to be regarded as an enlargement of the gullet for storage purposes. It is not digestive except in so far as salivary juice from the mouth may operate. Along with the food there may be water and mucus, and the fermentation may raise the temperature considerably. A thousand grains of oats have been reported from the crop of one wood-pigeon, and sixty acorns from another. In many cases the crop is seen to be over-crowded with fish, flesh, fruit, or foliage, and the bird may be seen working its neck in a way that suggests some discomfort in its repletion. Vultures may have to disgorge part of their booty before taking to flight; frightened pelicans and some other birds do the same, often on slight provocation. The skua gull utilises this tendency in order to get fishes from other gulls, and we have often seen a cat chase a wounded gull after its meal and secure what had been but recently swallowed. Regurgitation of food into the mouth of the young bird, *e.g.* in cormorant and petrel, shows how the abnormal may be normalised.

We have often watched an eagle working at the pieces of bird in its crop, including skulls and other pieces of skeleton, and though this is mainly to make itself more comfortable, it points to the regular habit most marked in owls, of separating the useful from the useless and ejecting the latter in pellets.

Mr. Beebe (1917, p. 130) describes the remarkable crop

of the Hoatzin of Brazilian swamps, a bird to which he has given special attention. The crop has become exaggerated at the expense of the stomach, and it has strong muscles in

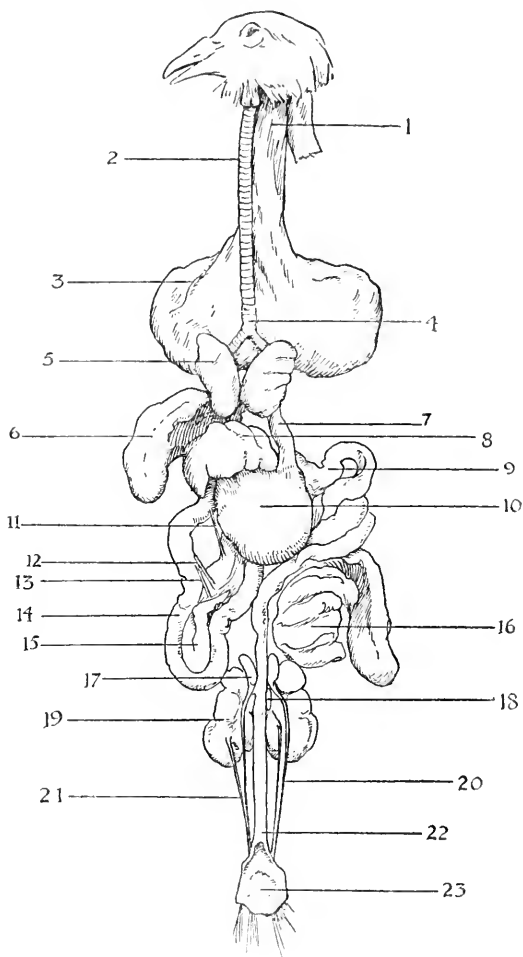


FIG. 24.—Dissection of pigeon's food-canal, etc. From a specimen. 1, gullet; 2, windpipe; 3, crop; 4, song-box; 5, lung; 6, liver; 7, proventriculus part of stomach; 8, part of liver; 9, part of small intestine; 10, gizzard; 11, 15, pancreas; 12, 13, two ducts of pancreas; 14, duodenum; 16, small intestine; 17, testis; 18, 22, rectum; 19, kidney; 20, vas deferens or duct of testis; 21, ureter or duct of kidney; 23, cloaca. The heart was removed.

its walls which are said to squeeze the juice out of the arum leaves on which the bird feeds. It has thus taken on a gizzard function, and it has become so large that the keel of the breastbone has had to give way in part to make room for it, and the clavicles are bent outward.

“**Pigeon’s Milk.**”—Many people suppose that there is something jocular about “pigeon’s milk”; others suppose that they know all about it. But there is no joke and there is no satisfactory understanding of what happens. “Pigeon’s milk” is a milky fluid with cheese-like solid particles, and it is produced in the crop of both sexes by a fatty degeneration and discharge of many of the cells of the lining epithelium. The milkiness is due to the fatty granules in the disintegrating discharged cells; the cheese-like particles are minute groups of discharged cells which have not degenerated so far.

As every one knows, the parents regurgitate the “milk” into the mouth of the young pigeon for some time after hatching, and the fluid doubtless serves as a readily digestible food until the young one is able to tackle more difficult material. In other words, it serves in gastric education. The regurgitation is mainly due to two special muscles which rise from the bird’s merryythought. It should be carefully noticed that the lining of the crop is not glandular, and that the pigeon’s milk is not a secretion. It is a discharge of lining cells which have undergone a peculiar transformation. The crop is an area for storage, not for digestion; but its worn and degenerate (we might almost say *moulted*) lining cells have come to have a use in the early nutrition of the young squabs. The same is said to be true of some parrots. It may be suggested that the discharge of the pigeon’s milk should be brought into line with the occasional moulting of the cuticular lining of the gizzard, and some analogous phenomena. But it is a desquamation and degeneration of cells, not a secretion or the liberation of a secretion.

At most seasons of the year it is possible to get some “pigeon’s milk” out of the crop, and perhaps there is an

almost continuous degeneration and replacement of the internal cells. But the amount of the milk is greatly increased during and immediately after incubation.

It is interesting to inquire whether the transformation and discharge of the cells lining the crop has any direct connection with the often extraordinary packing and distension of the crop with hard food. For that must exert a very unusual influence on the lining epithelium. Animals often exhibit a capacity for "normalising the abnormal"—witness the way in which the glutinous threads which exude from the male stickleback's kidneys are used to bind the leaves of fresh-water weed or fronds of seaweed into a nest. Is there some similar normalising in turning the pigeon's milk to account in the early nutrition of the young? In any case, it is obvious that we do not know all about pigeon's milk.

An interesting fact in regard to pigeon's milk has been discovered by MM. P. Champy and P. Colle (1919). There is a correlation between the activity of the crop and the gonads. During incubation the mucus membrane of the crop of both sexes thickens greatly, and continues to show cellular activity for fifteen days after the eggs are hatched. Now there is a reduction in the size of the testes and an absorption of material from the beginning of incubation onwards, and this coincides with the period of the multiplication of cells in the lining of the crop. Similarly, in the female there is during the brooding period an absorption of numerous young ova in the ovary. The investigators suggest that there is something in the way of a nutritive balance, there is an absorption of material in the gonads when there is expenditure of material on the part of the crop. This seems a plausible idea, especially as there is no trace of any hormone, but the matter requires further investigation, especially in view of the fact that the activity of the crop continues after the regression of the gonads has quite stopped.

The stomach of a bird may be a simple sac, but in most cases it is divisible into an anterior glandular portion (the

proventriculus) and a posterior muscular portion (the gizzard). John Hunter's experiment with a Herring Gull showed that after a year's feeding on grain, the stomach had become like a pigeon's gizzard. According to Edmondstone, the Herring Gull of the Shetlands changes the structure of its stomach twice a year, according to its food, which during the summer consists very largely of grain, and during the winter of fish. Semper notices in his "Animal Life" (1881, p. 68) that Edmondstone observed a similar change in the raven, and Ménériès in the owl (*Strix gal-laria*), while Holmgren made the converse experiment of feeding pigeons for a long time on flesh, with the result that their stomach became like that of a carnivorous bird.

These cases are very interesting because they illustrate the process of somatic modification in the individual. A change in the food is followed by a change in the structure. In the flesh-eating bird the wall of the stomach shows relatively little musculature and a strong development of glandular tubules secreting the digestive juice. In the grain-eating bird the musculature is particularly strong, and instead of the soft mucous membrane there is in the posterior region or gizzard the formation of a strong brown lining, with long filaments extending into the cavities of the tubules which run at right angles into the muscular layer. The proventriculus remains like the stomach of a carnivorous bird, with soft mucous membrane and glands.

Semper writes (1881, p. 414): "If the stomach of the pigeon is acted on for a sufficiently long period by feeding on flesh, the brown layer (called a cuticula) withdraws entirely from the tubules and is ejected; the tubules no longer secrete any solid matter, but only a fluid, and so become true glands. It would be interesting to ascertain whether the secretion now produced by these tubules in the gizzard is to be compared, chemically and with respect to its digestive qualities, to the gastric juice in the stomach of birds of prey. In gulls, on the other hand, which have become accustomed to a grain diet, the hitherto fluid secretion from the glands opening into the stomach becomes

rigid, and a more or less firm thick skin is formed in the interior of the stomach."

It must be understood, as Semper insists, that the two types of stomach are connected by inter-grades as well as by modifications, and that many carnivorous birds have as much gizzard as a pigeon or a hen. In the Little Grebe, the Crow, the Lapwing, and the Kingfisher there is a strong muscular wall and an internal, hard, brown pseudo-cuticle. In the recently fledged kestrel and in some other cases there is a transitory pseudo-cuticle.

The gizzard is a legacy from reptiles, for it is well developed in the crocodile. The typical features are: (a) the huge development of musculature on two opposite walls, numerous fibres radiating outwards from a central tendinous disc; (b) the bending of the sac upon itself so that the exit into the duodenum is not far from the entrance from the proventriculus; (c) the internal lining of pseudo-cuticula, really a secretion; and (d) the presence of pebbles which serve as grindstones. The contraction of the muscles of the two opposite walls brings these walls nearer one another, lessening the lumen of the gizzard, and the stones grind the food. In the course of time they get their corners rubbed off and slip down the duodenum. If they are not replaced by others, the bird goes out of health.

There are some remarkable peculiarities in gizzards. Some fruit-pigeons that eat nutmegs and the like have several score of hard conical projections on the pseudo-cuticle. The snake-bird, Anhinga, has a sieve of hairs at the duodenal end of the gizzard, which keeps fish-bones and the like from going through too quickly.

Mr. Beebe (1907, p. 140) tells how the lining of the gizzard in the male hornbill is ejected, forming a bag round the fruit which he has swallowed. "This, the male bird, in his native land, doubtless takes in his beak to the tiny opening of the walled-up nest and delivers into the bill of his mate. How admirable a spouse this, who not only seeks and provides sufficient food for his temporarily helpless family, but bears it to them wrapped up in a packet

torn from his very body—if not a ‘pound of flesh,’ at least enough to make a lunch basket.” In this and in similar cases the biologist has to link the extraordinary to the ordinary, for in many birds there is an occasional moulting of the lining of the gizzard.

H. C. Curl (1911) has studied the periodically ejected lining of one of the hornbills (*Hydrocorax hydrocorax*), and finds that it consists of a tough homogeneous secretion from the glands of the stomach. It comes away along with a certain amount of undigested refuse.

The Intestine and its Annexes.—The stomach is followed by the duodenum into which there open the two or three ducts of the pancreas, or stomach sweetbread. The presence of three ducts, as in the pigeon, is an index to the fact that the gland has a threefold origin in the embryo. For the pancreas, like the liver, arises as an out-growth from the mid-gut (or mesenteron); it is, to begin with, saccular—lined with endoderm and surrounded externally with mesoderm.

The use of the pancreatic juice is to continue the digestive action of the stomach. The comminuted “chyme” from the gizzard is acted on by three pancreatic ferments, one changing starchy food into sugar, another changing protein into peptone, and a third emulsifying the fat and changing it into fatty acids and glycerol. In this way the chyme becomes chyle. The absorption of the digested food is greatly facilitated by the thousands of finger-like villi projecting into the lumen of the gut, from the stomach to the end. The sugars and the peptones pass into delicate tributaries of the mesenteric veins which enter the villi; and these mesenteric veins combine in a hepatic portal vein which breaks up in the liver. But the villi also contain fine tributaries of the lymphatic vessels, and into these the digested fat passes. The lymph vessels eventually open into the venous system.

The liver is usually the largest organ in the body; it communicates by two or three ducts with the duodenum and one of the ducts is typically connected with a

gall-bladder which stores the bile secreted by the liver. The gall-bladder is absent in many pigeons and parrots. In most cases the liver is a two-lobed organ, and the apex of the heart fits in between the two lobes.

As to the uses of the liver, one may say briefly (1) that it serves as a great intermediating sponge between the digested sugars and proteins, brought to it by the portal system, and that by keeping back certain things, *e.g.* surplus sugar, it maintains a certain constancy of composition in the blood, which would otherwise be apt to change after each variation in meals. (2) Surplus sugar is stored in the form of animal starch or glycogen—a reserve food for the muscles. (3) The bile is largely of the nature of a waste-product, but it is of some slight service in connection with digestion. (4) The liver also begins the elimination of nitrogenous waste-products from the blood—the work which the kidneys complete.

In reference to the presence or absence of a gall-bladder, it has been shown by Richard E. Scammon (1916) that in the pigeon the gall-bladder is developed to all appearance in a perfectly normal way. Later on, in the majority of cases at least, it is completely lost, though its duct persists and grows to some size in further embryonic development. There is a larger anterior hepatic duct which is not associated with the gall-bladder or its duct at all, but conveys the bile independently from the liver. There are other animals besides ordinary pigeons in which the gall-bladder is absent, such as lamprey and rat, but the reason for its disappearance or absence is unknown. Even in man it is occasionally absent. Scammon calls attention to the large size of the bile-ducts in the embryos of both pigeon and rat, and suggests that this may be a compensation for the absence of the usual bile reservoir in the form of a definite sac.

The coiled part of the intestine following the U-shaped curve of the duodenum is known as the ileum, and it continues the twofold work of digestion and absorption. Digestion in birds is singularly perfect, as may be inferred from the extreme shortness of the large intestine or rectum,

which contains relatively little undigested or indigestible food. Another reason is that many birds are very selective in their eating, and do not take much that they cannot use. A third reason for the extraordinary shortness of the large intestine may perhaps be found in the habit owls and many birds of prey have of casting pellets of indigestible materials from their crop.

The twofold problem of a food-canal is to digest and absorb, and the looping of the bird's ileum is a fine example of close packing. Great length is made possible without great bulk. Professor Newton made a special study of the intestinal looping, and some of his results are very instructive (1893, p. 140).

"In early embryonic stages the intestinal canal is a straight tube ; but, as its growth proceeds far more rapidly than that of the body-cavity, it is necessarily thrown into folds or loops. Moreover, since it is suspended from the vertebral column by the mesentery, or lining of the body-cavity, its several folds are thereby connected with one another in various ways, and their number and shape depend to a great extent upon the space available in the cavity, as well as upon the shape, size, and position of the stomach and neighbouring organs ; but the various ways in which the small intestine is stowed away in different birds exhibit types so definite and constant that they cannot be considered accidental or meaningless features."

The fact is that the mode of looping is very diagnostic of relationship ; it has great " taxonomic value." In related birds there are similar patterns, and some of the divergent cases are exceptions that prove the rule, for in some cases they can be correlated with disturbing peculiarities of diet. It is very interesting to find that old loops may be lengthened out and new ones intercalated without disturbing a typical intestinal pattern characteristic of families or groups of families. "The highest and perhaps newest mode of stowing an increased amount of intestinal length is that in which one of the folds already existing is lengthened and, owing to its intestinal growth, turns into a spiral ; in this

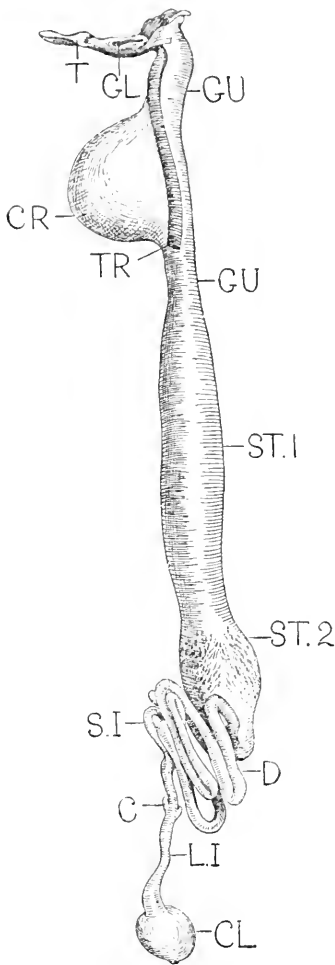


FIG. 25.—Food-canal of an eagle. From a specimen. T., tongue; GL., glottis; GU., gullet; CR., crop; TR., cut end of trachea; ST.1, anterior part of stomach; ST.2, posterior or pyloric part of stomach; D., duodenum; S.I., small intestine; C., cæca; L.I., large intestine or rectum; CL., cloaca.

way the other loops will undergo the least possible disturbance" (Newton, 1893, p. 144).

At the junction of the ileum or small intestine with the rectum or large intestine there is a valve (ileo-cæcal), preventing a return of the contents, and there are usually two blind diverticula, the cæca. In rare cases, *e.g.* herons, there is only one; in rarer cases, *e.g.* some parrots, there is none. The cæca occur in all sizes, from mere vestiges, *e.g.* in the pigeon, to long functional tubes, as in the duck. In the ostrich the cæca are not only very large, but they contain a spiral valve. When the cæca are large enough to be of use they serve as cul-de-sac in which the food is delayed in its downward passage. "It is probable that in them certain hitherto undissolved matter, as cellulose and possibly chitin, is acted upon by marsh-gas, so as to extract as much nutrition as possible from the food" (Newton, 1893, p. 187).

There is a great diversity as regards the cæca, as has been shown in detail by Magnan (1911). They are absent in parakeets and some hornbills. In the latter the mucous

membrane is much modified at the spot where they should arise. They are minute in many birds, *e.g.* pigeons; of considerable size in many birds, *e.g.* ducks. They attain to a length of 85 cm. in the male capercaillie. Sometimes there is only one, as in some fish-eating birds; usually there are two; there is a third cæcum in many ducks and birds of prey. This is continuous with the gut to start with. But it has been shown by A. Lelièvre and E. Retterer (1910) that the glandular epithelium of the third cæcum diverges from that of open glands; it gives rise to a mass of reticular tissue producing fluid and corpuscles, which pass into the blood. In abnormal double-legged ducks and fowls there may be a third cæcum—a curious visceral duplication accompanying that of the part of the skeleton.

The walls of the intestine are composed of five layers:—

(1) An outer tunic of connective tissue, partly elastic;

(2) Circular smooth muscle;

(3) Longitudinal smooth muscle;

(4) A submucosa with blood-vessels, lymph-vessels, and nerves imbedded in loose connective tissue; and

(5) The digestive and absorptive endodermic epithelium.

A villus is an ingrowth of (4) and (5). There is often an opening of a tubular digestive gland between one villus and another. It is a little point of some interest that in Mammals the longitudinal muscular layer is outside the circular, which is enough to show that Mammals and Birds are on different tacks of evolution. As regards

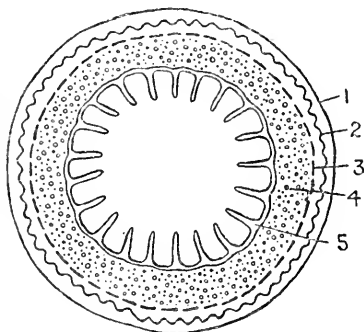


FIG. 26.—Diagrammatic cross-section through the intestine of the bird. 1, outer investment of connective tissue; 2, circular smooth muscle; 3, longitudinal muscle; 4, connective tissue with blood-vessels, lymph vessels, and nerves; 5, digestive absorptive epithelium, with villi into which ingrowths of (4) also extend.

the two muscular layers, Birds and Reptiles resemble one another.

The cloaca or terminal chamber is vaguely divided into three regions :—

- (a) That which receives the rectum,
- (b) That which receives the ureters from the kidneys and the reproductive ducts, and
- (c) The terminal portion.

From the dorsal side of the terminal portion of the cloaca there grows out a rather enigmatical hollow pouch called the Bursa Fabricii. Its development has been followed by Lelièvre and Retterer (1910) and Jolly (1911). The internal epithelial lining gives off buds which penetrate into the envelope of the pouch. These buds or "closed follicles" become the seat of the formation of numerous white blood-corpuscles and lymph-corpuscles. Gradually, however, the blood-forming ceases; the buds are changed into reticulated tissue; the adult organ is practically a retrograded mass of fibrous connective tissue. It may become quite hard.

§ 4. PHYSIOLOGICAL SUMMARY

Looking backwards, let us think of the whole matter physiologically. The food consists of carbohydrates, fats, proteins, and "accessory substances" or vitamins. It is used for growth, for repair, for storage purposes, and as a fuel affording energy for work. There is no particular form in which proteins can be stored except in so far as they are incorporated into the living tissues of the body. The storable material consists of carbohydrates and fats. The proteins are broken down into amino-acids (with formation of nitrogenous waste) and these are used for growth, repair, and combustion. Digestion is the process of dissolving the food, making it more diffusible and available. The solid carbohydrates are changed into fluid sugar; the fats are split up into fatty acids and glycerol; the proteins are changed into peptones. The ptyalin or amylase of the

saliva may change starch into maltose ; the gastric juice of the stomach converts proteins into peptones ; the pancreas has three ferments—a diastatic one affecting starch, a tryptic one attacking proteins, and a lipase working on fats. The digested sugars and peptones are gathered up from the stomach and intestine by mesenteric veins, which unite to form the portal system entering the liver. In this great filter the digested food carried by the blood is so treated that surplus materials are kept back, thus extra sugar is retained as glycogen, and poisonous stuffs are sifted out. The hepatic veins lead the blood from the liver into the top of the great inferior vena cava, and thus into the heart and the general circulation. The digested fats are collected from the intestine by the lymphatic vessels, and pass thence indirectly into the venous system. The final steps are the utilisation of the digested food, as already stated, for growth, repair, storage, and direct combustion.

CHAPTER VI

THE INTERNAL ECONOMY OF THE BIRD'S BODY

§ 1. The Master-Activities. § 2. Muscular Activity. § 3. Nervous Activity. § 4. The Sustentative Functions. § 5. Respiration. § 6. Excretion. § 7. The Uses of the Blood. § 8. Warmbloodedness. § 9. The Regulatory System and the Resulting Correlation.

A VORTEX-RING from the chimney of a locomotive or a smoker's mouth persists for some minutes in its atmospheric environment. A whirlpool in a river remains the same for years though its actual material is changing every second. A living creature is also a wondrous eddy of vortex-rings, enchanted into unity ; and physiology is an inquiry into this enigma of persistent integrity in spite of ceaseless change. The aim of this chapter is to *illustrate* what we may venture to call the orchestration of the bird's body—and does it not find its highest expression in the music of Spring ?

§ 1. THE MASTER-ACTIVITIES

It is plain that there are two master-activities in the animal body, namely, *moving* and *feeling*, the functions of the muscular and the nervous system respectively. To promote these two functions, often termed contractility and irritability, is the task of all the other everyday functions, such as digestion, respiration, and excretion. They are sustentative, or subsidiary, or auxiliary ; they are not ends in themselves like moving and feeling. The reproductive function is in a different category.

At the same time, it must be admitted that there is a very real sense in which the alimentary system commands

the neuro-muscular. As some would say, the "autonomic" alimentary system rules the "projicient" neuro-muscular system. The demands of hunger compel the bird to hunt, and modern psycho-physiological work has shown that this is a far-reaching fact. The apparent slave is often the real master.

§ 2. MUSCULAR ACTIVITY

All movements in higher animals are due to muscles, whether locomotion when one piece of skeleton is pulled nearer another, or the beating of the heart when a cavity is lessened by the contraction of its walls. In slowly moving parts of the body, notably the food-canal, the muscle-cells are "smooth" or non-striated—small spindle-shaped cells, dovetailed into one another and united by cement substance. In the wall of the food-canal they cause peristalsis; that is to say, their slow contraction gradually presses the food onwards. When there is a violent action, as when the frightened petrel squirts out oil from its mouth, the muscles used are outside the wall of the food-canal, and these are striped and quickly contracting. In backboned animals almost all the muscles, except those in the wall of the gut, the wall of the bladder, and the walls of the arteries, are of the striped or striated type, and the bird is unsurpassable in its muscularity.

The biological note here is of some interest. The most primitive muscle-cells, seen around the exhalant pores of sponges, are spindle-shaped unstriped cells. These are common in many sluggish backboneless animals, such as tapeworms and oysters. They are well represented in the border-line animals, the Ascidians or Sea-Squirts. In the very interesting annectent type *Peripatus*, which does something to link insects back to Annelid Worms, all the muscles are unstriped save the quickly moving muscles of the mandibles. Now the point is this, that in backboned animals the primitive slowly contracting type of muscle-cell lingers in such places as the wall of the food-canal, precisely in places where slowness of contraction is useful.

In normal circumstances striped muscle contracts only when impulses come to it from the central nervous system ; but smooth muscle has an automatic activity, being able to contract, apart from the central nervous system, under the influence of local stimuli. The term "involuntary," often applied to smooth or unstriped muscle, is apt to suggest that it is not under the control of the central nervous system, which is far from being the case.

When a muscle contracts, *e.g.* in bringing the bird's wing down, two very distinct processes occur. There is potential energy in the resting muscle, in the form of surface energy or osmotic energy, or both, and this is used to develop tension which does work. In this physical process, which might be compared to the uncoiling of a spring, lactic acid is let loose from the muscle-substance. As Professor Bayliss says : " If we compare the muscle to a gas engine, the lactic acid corresponds to some essential moving part, say the piston, which merely undergoes change of position. Its change of position, however, leads to the liberation of energy " (1915, p. 446).

The second chapter is putting the lactic acid back into the muscle so that it may contract again. This requires the oxidation of a carbohydrate (*e.g.* blood sugar) or, it may be, fat, which supplies the energy for the restoration of the lactic acid. Much oxygen is used up in this combustion, carbon dioxide is given off, and heat is evolved. This is the chemical phase of the process of contraction, succeeding the physical phase. It appears that practically the whole of the tension can be used to do work, but that about 50 per cent. of the energy of the second phase is lost as heat.

The important general fact, established by Fletcher and Hopkins, is that the contraction of a muscle must be separated into two chapters—a predominantly physical chapter, without combustion, but with a displacement of lactic acid, and a predominantly chemical chapter, centred in an explosive combustion, as the outcome of which lactic acid is replaced.

To quote again from Professor Bayliss : " The muscular

system is analogous to that of a gas engine used to compress air into a reservoir, from which it is taken to drive, by its pressure, various machines and tools. 'The energy of the oxidation of the fuel is not used from the engine directly' (1915, p. 462).

The muscles of birds are specialised in many ways, *e.g.* in moving the wings and neck, in contracting the gizzard if there is one, in clinching the toes in perching, but careful investigation has shown that the raw materials, as it were, are in the main represented in reptiles. Very remarkable, however, is the fact that the muscles concerned with flight may be so strongly developed that they amount to half the whole weight of the bird.

It must be kept in mind that the muscles, besides being the engines of the body, still rather mysterious in their operations, are also the producers of the animal heat which plays an important part in the internal economy. The production of animal heat compensates the body for what is lost to the outer world—especially in the hot breath and by radiation from the skin, feathered though it is, and it thus saves the bird from cooling down so far in cold weather that vital processes would be stopped by the freezing of fluids. But it has also a *positive* importance in facilitating various chemical reactions which are always going on in the routine of metabolism; thus heat accelerates an oxidation process. The animal heat has also a part to play in the physical processes that go on in the body. Thus it lessens the friction of body-fluids like the blood, and makes diffusion easier.

§ 3. NERVOUS ACTIVITY

The nervous system consists of the brain and the spinal cord and the nerves issuing from these, with in addition the sympathetic nervous system, which has particularly to do with the superintendence of the viscera. The chief functions of the nervous system are (1) to receive messages from the outer world through the sense-organs, so that

(2) the organism may adjust itself effectively to its environment by controlled movements, and (3) to bind the body into one (integration) so that each part, through the central

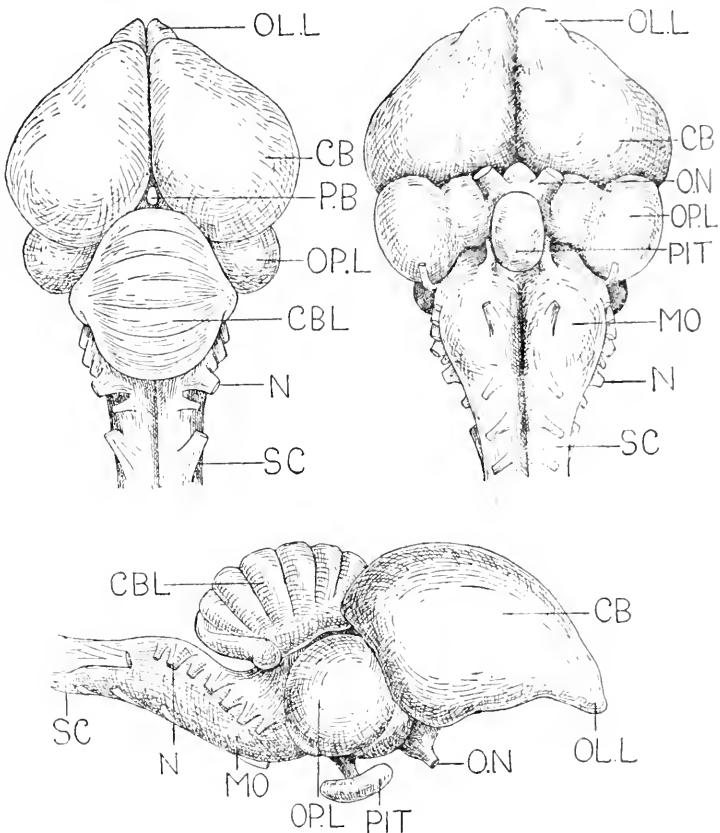


FIG. 27.—The brain of a pigeon, seen from above, from below, and from the side. From a specimen and model. OLL., olfactory lobes; CB., cerebrum; P.B., pineal body; O.P.L., optic lobe; CBL., cerebellum; N., nerve issuing from spinal cord (S.C.); O.N., optic nerves crossing as they enter the brain; PIT., pituitary body; M.O., medulla oblongata.

system, can be connected up with any other, and so that the numerous vital activities are harmonised.

The nerve-fibres, which compose the nerves, may be

compared to the wires of a telephonic system. The nerve-cells, which compose the centres or ganglia, may be compared to individual telephones which receive news (sensory stimuli) from far and near and likewise issue orders to executive parts such as the muscles. A comparison may be made between the chief nerve-centres, say in the brain, and the "central office" of the telephone system, where messages may be shunted and connections established. But the comparison must not be pressed far, else it breaks down badly. The central nervous system *stores* messages in its nerve-cells, but this is not allowed in a telephonic exchange; and the central nervous system *co-ordinates* messages, combining them and allowing them to influence one another, which is also quite unpermissible in the telephonic "central."

It must also be noted that nerve-fibres are outgrowths of nerve-cells or neurones. There are not two units—the nerve-fibre and the nerve-cell; there is but one—the neurone. This gives off in typical cases (1) a number of short protoplasmic processes or dendrites which link up with similar processes from another neurone, and (2) an axis-cylinder or main fibre which is often long and carries commands to muscle or gland or brings in messages from a distant external or internal part.

A ganglion or nerve-centre is a collection of neurones in intimate linkage with each other. A nerve is a bundle of nerve-fibres within a sheath, and sensory nerve-fibres which carry messages to the centre must be distinguished from motor nerve-fibres which carry commands outwards. The nature of the message or of the command that "travels" along a nerve-fibre remains an enigma.

A Reflex Action.—Not even an elementary understanding of the activity of the nervous system is possible without knowing what is meant by a reflex action. In backboned animals, such as birds, its typical expression—the outcome of a long evolution—is as follows. A nerve issuing from the spinal cord is made up of dorsal and ventral roots. The dorsal roots (otherwise called posterior or

afferent) are made up of portions of sensory neurones, carrying messages inwards (as the diagram suggests). The ventral roots (otherwise called anterior or efferent) are made up of portions of motor neurones, carrying commands outwards. Outside the spinal cord, on each dorsal root, there is a spinal ganglion (SP.G.), and this consists of sensory neurones. From each of these a fibre runs into

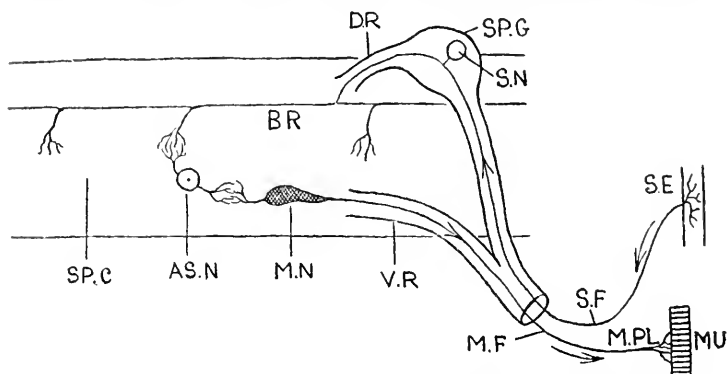


FIG. 28.—Diagram of the elements involved in a reflex action. SP.C., the spinal cord; AS.N., an associative neurone; M.N., a motor neurone; V.R., a ventral root of a spinal nerve; M.F., a motor nerve-fibre ending in a motor plate (M.PL.) on a muscle (MU.); S.E., ending of a sensory nerve-fibre, e.g. on the skin; S.F., a sensory nerve fibre; SP.G., a spinal ganglion on a dorsal root (D.R.) of a spinal nerve; S.N., a sensory neurone in the spinal ganglion; BR., branches of a sensory nerve-fibre within the spinal cord. The arrows indicate the direction of the message or command. Branches of a sensory fibre come into close contact with branches of an associative neurone; and similarly there is close contact or synapsis between other branches of the associative cell and those of a motor neurone.

the spinal cord and another runs out to the periphery, terminating in a sensitive nerve-ending on the skin or in a sense-organ. The ventral roots are made up of nerve-fibres, each of which grows out from a motor neurone in the spinal cord and is continued to a nerve-ending on a muscle or, it may be, to a gland. Finally, as middlemen between the internal branches of the sensory nerve-fibres and the internal branches of the motor neurones, there are associative neurones (otherwise called communicating or internuncial). Thus we have, as in figure 28 :—

- (1) a peripheral nerve-ending (S.E.),
- (2) a sensory or afferent nerve-fibre (S.F.),
- (3) a sensory cell-body in a spinal ganglion (S.N.),
- (4) a sensory nerve-fibre branching in the spinal cord (BR.),
- (5) an associative neurone with its branches (AS.N.),
- (6) a motor neurone (M.N.),
- (7) a motor or efferent nerve-fibre (M.F.), and
- (8) a nerve-ending (M.PL.) on a muscle (MU.).

The mother bird touches with food the bill of its half-asleep nestling and instantly, before we can say "reflex action," the mouth is open wide. Then follow other reflex actions of swallowing and the like.

A sensory message entering the spinal cord may affect an associative neurone which passes on the stimulus to a motor neurone, but it may affect more than one, so that another motor neurone is called into action, or so that the most direct answer-back is inhibited by a counteractive influence. For reflexes are not quite obligatory, as we know when we smother a cough or inhibit a sneeze on a solemn occasion.

Reflex actions, such as opening the mouth at the touch of food, or gripping the food with the pharynx, or violently squirting out nauseous stuff when startled, or shutting the eye when a blow is threatened, play an important part in the life of birds. They are inborn; they do not require to be learned; they are due to pre-arranged linkages of certain nerve-cells with certain muscles; they are often bound together in a sequence so that one pulls the trigger of another; in their simplest forms they do not require the activity of the brain, only of the spinal cord.

The diagram of the bird's nervous system shows the relatively large brain sheltered by the skull, the long spinal cord sheltered by the neural arches of the vertebræ, and the numerous cranial and spinal nerves. Some of the cranial nerves are purely sensory, such as the optic which carries impressions from the retina to the brain; others are purely motor, such as the oculomotor which is in command of four of the six muscles that move the eye-ball; and others are

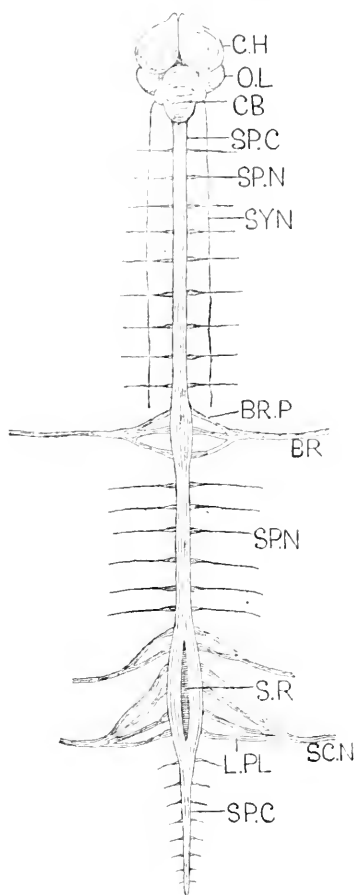


FIG. 29.—Nervous system of a pigeon. From a specimen. C.H., cerebral hemispheres of the brain; O.L., optic lobes thrust to the side; CB., cerebellum; S.P.C., spinal cord; S.P.N., spinal nerves; S.Y.N., sympathetic nervous system; B.R.P., brachial plexus to wing; S.R., rhomboidal sinus in the dilated spinal cord (S.P.C.); L.P.L., lumbar or sacral plexus of nerves uniting to form the sciatic nerve (S.C.N.) going down the leg.

composed of both sensory and motor nerve-fibres, as in the case of the vagus which goes to heart, stomach, and many other parts, controlling these, but also receiving tidings from them. The spinal nerves, as already indicated, are mixed nerves, with sensory and motor components.

There is on each side of the backbone a chain of sympathetic ganglia. These give off fibres to the adjacent viscera and blood-vessels. They are connected to one another in a chain, which is anteriorly linked to the brain. Each is also connected by a fine nerve-thread with the ventral root of a spinal nerve.

As to the brain itself, it is in great contrast to that of reptiles, for it fills a spacious cranial cavity. The cerebral hemispheres are large, but they are not convoluted as in most mammals. Their roof is rather thin and their main mass consists of large corpora striata which bulge into the ventricles. The cerebral hemispheres meet the cerebellum dorsally and throw the solid optic lobes to the sides. To begin

with, these optic lobes lie in the middle line as in fishes, but they are gradually shunted outwards and downwards by their own growth and that of the adjacent parts. The olfactory lobes in front of the cerebral hemispheres are very small, in correlation with the poorly developed sense of smell. A slight posterior separation of the cerebral hemispheres will disclose the region of the optic thalami. From this region in the embryo the eyes grow out, and it also gives origin to the pineal body above and the pituitary body below. The cerebellum is large, ridged transversely, and divided into a median lobe and two small lateral lobes. It has in part to do with the control of movements. In a fish the brain lies quite flat; in birds it has a marked curvature, and the medulla oblongata is hidden below the cerebellum. There are, thus, five chief parts of the brain—the cerebral hemispheres, the optic thalami, the optic lobes, the cerebellum, and the medulla oblongata.

Pineal Body.—On the roof of the bird's brain, between the cerebral hemispheres and the cerebellum there lies a small reddish body, the pineal body. It is borne on the end of a stalk or epiphysis, which arises as usual as a pouch-like diverticulum from the roof of the optic thalami region, and afterwards becomes ampulla-like. Funkquist (1912) notices that the simple ampulla form is retained in the sparrow, and that in divers and ducks tubules arise as buds from the floor of the pouch, which may be subsequently constricted off. It is an epithelial organ to start with, but is modified into neuroglia, and is invaded by connective tissue septa with blood-vessels. In some cases, *e.g.* canary, the tubules remain hollow; in other cases, *e.g.* fowl, the lumen is more or less completely obliterated. Apart from fine nerve-threads accompanying the blood-vessels, there is no trace of nerve-cells or nerve-fibres in the pineal body of birds.

In some of the lower Vertebrates, *e.g.* lampreys, the dorsal outgrowth from the roof of the optic thalami is distinctly *paired*. There is (1) a pineal organ or epiphysis proper, and there is (2) a parietal organ which arises from (1) or independently in front of it. Perhaps they were originally

the right and left members of a pair. In lampreys both the epiphysis and the parietal organ show an eye-like structure at the tip, most marked in the case of the epiphysis. In the so-called New Zealand lizard and in some other reptiles the eye-like structure is borne by the parietal organ. In birds "the pineal body," which has no trace of optic function, corresponds to the parietal organ.

On the under surface of the optic thalami region there is a downgrowth (the cerebral part of the hypophysis) which meets an upgrowth from the mouth (the oral part of the hypophysis). The two components unite to form the enigmatical pituitary body, which loses all connection with the mouth and rests on the basisphenoid bone. It is partly glandular and partly nervous, and it forms an internal secretion or hormone which is swept away by the blood and distributed through the body—a subject to which we must return later.

The spinal cord passes downwards in the protected tunnel formed by the neural arches of the vertebræ, and gives off numerous nerves. Very noteworthy are the strong nerves forming the "brachial plexus" for the wing and its muscles, and the corresponding "sacral plexus" forming the sciatic nerve which passes down the leg.

In the pelvic region of the spinal cord there is an interesting dilatation, leaving a median sinus. The expansion is highly differentiated and no doubt connected with the bipedal habit and the consequently increased importance of the innervation of the hind leg. It is manifested (Imhof, 1905) at a relatively late period in embryonic life—which points to its being a secondary acquisition.

§ 4. THE SUSTENTATIVE FUNCTIONS

The master-activities of the bird's body are those of the muscular and nervous systems. Most of the other functions may be called sustentative or subservient to these, always excepting growth and reproduction which stand by themselves. The master-activities imply wear and tear

and the formation of waste-products. The energy used and the energy lost must be made good again, and that is effected by taking in food. But this food must be prepared within the body and altered both physically and chemically, so that it may be used to the best advantage. This has been already discussed. Many different chemical processes go on in the body, but for the production of energy and the doing of continued work oxidations are essential. Thus the function of respiration implies the capture of oxygen and the elimination of the poisonous carbon dioxide. The filtering out of other waste-products which would clog and poison the system is the function of excretion. Then there is the regulative function in so far as that is effected by the chemical messengers of the ductless glands. Let us turn to these functions of respiration, excretion, and regulation.

§ 5. RESPIRATION

The breathing of birds is in several respects peculiar ; it is specialised in relation to flight, to song, and to intense activity in general. Some of the important peculiarities are the following : the lungs though relatively small and hardly distensible, have a large internal surface for gaseous interchange ; the driving out of the air is assisted by the strokes of the wings ; expiration is the active part of the respiratory process, not inspiration as in mammals ; the lungs open into a system of air-sacs which economise the work of breathing and have other uses, though they are quite unimportant in making the bird more buoyant.

At the back of the tongue on the ventral surface is the glottis, the opening of the windpipe or trachea. It does not show more than a slight hint of the epiglottis, the movable lid characteristic of mammals, familiarly useful in keeping food from going down the wrong way.

The glottis leads into the larynx, which is supported by the usual (3) cartilages, but is remarkable in having no vocal cords, for in birds these are in the syrinx at the foot

of the windpipe. The cartilages of the larynx are biologically interesting, for they are the transformed representatives of branchial arches—an instance of a common method of

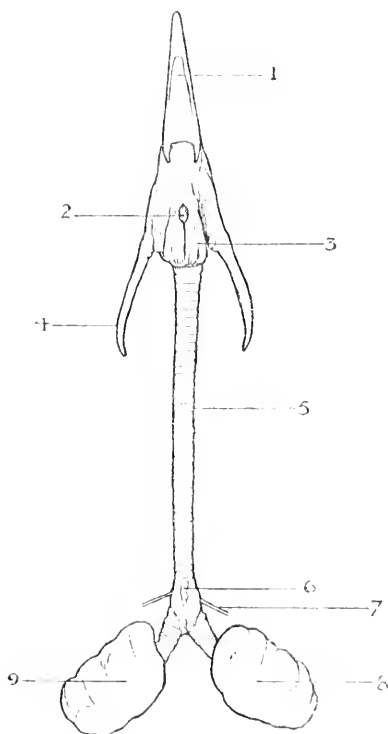


FIG. 30.—Part of breathing system of a bird. From a specimen. 1, the tongue; 2, the glottis or entrance to windpipe; 3, the voiceless larynx; 4, posterior "horns" of the hyoid, to which some tongue muscles are attached; 5, the windpipe; 6, the syrinx or song-box; 7, two muscles moving the syrinx; 8, 9, the lungs

organic evolution, making a new thing out of an older thing. The larynx and the vocal cords began in Amphibians.

The trachea is supported by bony "rings," usually, but not always, complete. In mammals the rings are gristly. The trachea is sometimes much longer than the neck; it is coiled inside the breastbone in the Whooper Swan, outside the breastbone in the Capercaillie. It is moved by two sterno-tracheal muscles attached to the front of the breast-bone.

The syrinx or song-box at the base of the trachea is absent in ostriches, storks, and some vultures. It is an enlargement of the base of the trachea and of the first two or three rings of the bronchial tubes, and it contains the stretched vocal cords which vibrate

more or less musically when the expired air passes rapidly over them. There is a somewhat complex skeleton and musculature. There may be an asymmetrical accessory chamber or labyrinth in addition to the main cavity or

tympanum. It is again of biological interest to notice that while the syrinx is a new structure, and peculiar to birds, it is in reality a transformation and complication of the base of the trachea and the beginning of the bronchial tubes.

The main chamber, as we have mentioned, is called the tympanum. It is traversed horizontally by a projecting bony band called the pessulus, and this forms a partition

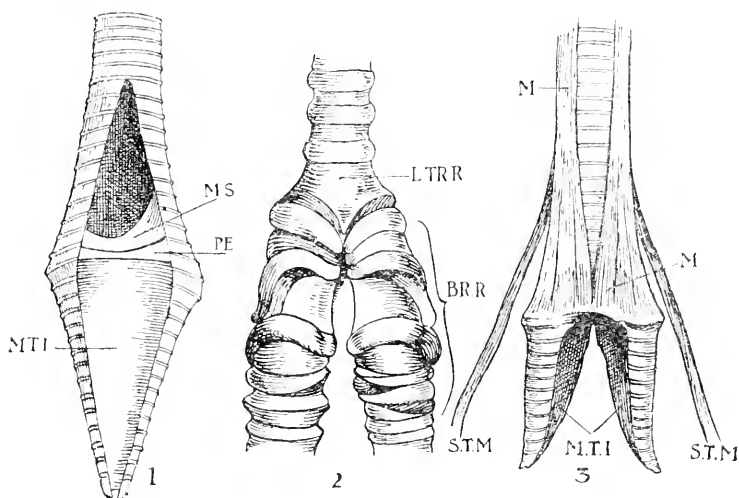


FIG. 31.—Syrinx of raven (after Owen). 1. Side view laid open; PE., the bony band or pessulus; M.S., membrana semilunaris, a fold supported on the pessulus; M.T.I., membrana tympaniformis interna, the internal wall of a bronchus. 2. Syrinx after removal of muscles; L.T.R.R., last modified tracheal ring; B.R.R., three first modified bronchial rings. 3. Front view of syrinx with muscles (M.), and sternotracheal muscles (S.T.M.), extending from the trachea to the sternum; M.T.I., membrana tympaniformis interna.

between the anterior openings of the two bronchial tubes. It gives off on each side two arched processes, dorsal and ventral, which run down the bronchial tube. Between these two horn-like processes the membranous wall of the bronchial tube is stretched, forming the membrana tympaniformis interna. In singing birds there is another membrane, the semilunar, attached to the pessulus, and there may be another on each side of the glottis. These

membranes function as vocal cords. Their tension is regulated by muscles attached to the wall of the syrinx.

A detailed account of the syrinx of the common fowl has been given by A. O. V. Tymms (1913), who emphasises the following features. There is an extensive syringeal

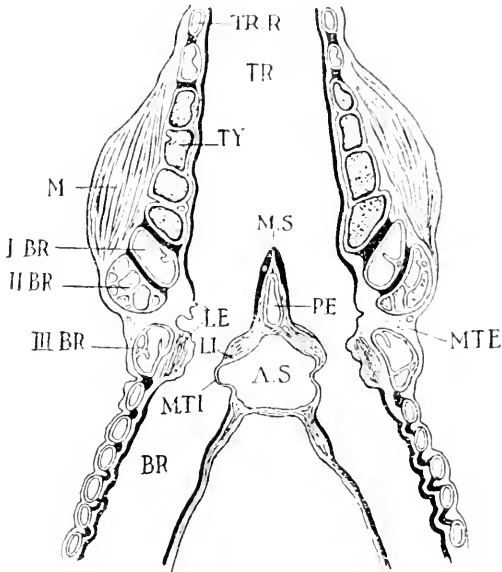


FIG. 32.—Vertical section of the syrinx of a male blackbird (after Haecker). TR., trachea or windpipe; TR.R., a tracheal ring cut across; TY., wall of tympanum or general cavity of the syrinx; M., muscles on the wall; I.B.R., 1st bronchial ring; II.B.R., 2nd bronchial ring; III.B.R., 3rd bronchial ring; BR., bronchus; PE., bony pessulus; M.S., membrana semilunaris; A.S., cavity occupied by an extension of the anterior thoracic air-sac; LE., external lip or labium; LI., internal lip or labium; M.T.I., membrana tympaniformis interna; M.T.E., membrana tympaniformis externa.

chamber or “tympanum” with membranous walls; the last five tracheal rings are very vestigial, the first two bronchial semi-rings are more strongly developed, the pessulus is bolt-like, with ventral and dorsal triangular plates; very noticeable is the absence of muscles in direct or intimate association with the syringeal membranes; there

is a complex and intimate relationship between air-sacs and syrinx.

The short bronchi divide up in a peculiar fashion to form the lung. A main stem goes right through as the mesobronchus and leads into the abdominal air-sac. Near its end it gives off a branch which leads into the post-thoracic air-sac. But soon after it enters the lung the main stem shows a dilatation or vestibule, and this gives off a number (four in the pigeon) of secondary bronchi or ectobronchia. These lead into other air-sacs—an interclavicular, two cervicals, and two anterior thoracics.

From the mesobronchus and the ectobronchia there arise tertiary bronchi, some of which unite with one another. They give off minute canaliculi, through the walls of which there is gaseous interchange with the blood.

There is a median vertical septum of connective tissue between the two lungs, and this is continuous with a fibrous connective tissue "pleural membrane," which covers the ventral surface of the lungs and binds them at their edge to the thoracic wall. The dorsal attachment of the lungs to the ribs is in part muscular. This envelope of the lungs bears some resemblance to the muscular diaphragm of mammals, but there is no homology. It does not shut off the "chest" from the visceral cavity, for the air-sacs go through it; moreover, the pericardial space in which the heart lies is quite outside it. What has been called "the oblique septum" in birds simply consists of the walls of the air-sacs in so far as these protrude into the body-cavity and are not adherent to the body-wall.

The air-sacs are like soap-bubbles; they are ciliated internally; they have few blood-vessels on their walls. As they are full of hot air, they must make the bird a little more buoyant, but so little that the lightening is counteracted by a few mouthfuls of solid food. Their functions are not in this direction. They considerably increase the content of air which a bird has in its respiratory system, and this is useful in the prolonged immersion of diving birds and in enthusiastic song. But there is a further

advantage. When the cavity of the thorax and abdomen is lessened by a raising of the sternum, and it may be a lowering of the fused dorsal region of the vertebral column if the bird is flying, the air is driven out of the lungs. But

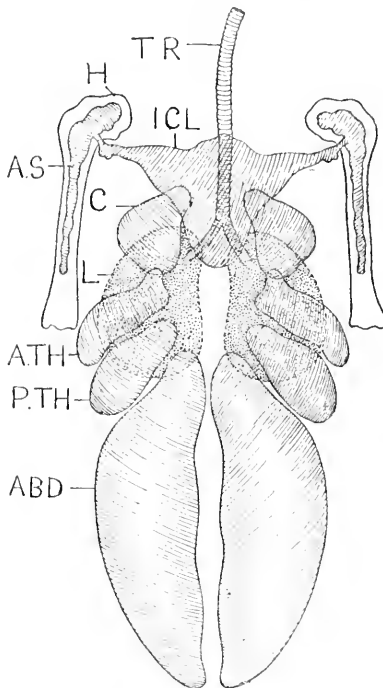


FIG. 33.—The system of air-sacs in a bird. L., the right lung; C., a cervical air-sac; I.C.L., the interclavicular; A.S., an outgrowth into the humerus (H.); A.T.H., anterior thoracic air-sac; P.T.H., the posterior thoracic; A.B.D., the abdominal air-sac; TR., the trachea or windpipe.

this also implies that non-ventilated air passes into the lungs from the air-sacs. When the rebound comes and the cavity of the body increases again, air rushes into the lungs and some of it fills the air-sacs. Thus in every complete respiratory movement there is a *double* tide of air into and out of the lungs. Or, to put it in another way, the tidal air is renewed twice in every respiratory act.

Another function of the air-sacs is to promote internal perspiration and thus help in regulating the high temperature of the body. Most birds take much water, but there is little water in their urine, which is semi-solid, and they have no sweat-glands like mammals. Hence the advantage of the internal surfaces of the air-sacs,

for water-vapour diffuses from the blood into the cavities and passes out by the lungs.

Some investigators of the air-sacs of birds think that their importance in connection with respiration has been over-rated. Thus B. Müller (1907) maintains that the

air-sacs have no positive function, but are rather to be thought of as empty spaces whose value lies in their emptiness. They facilitate the movements of the organs in the thorax, especially the heart. This view over-emphasises one aspect.

A good account of the detailed structure of the bird's lung is given by A. Juillet (1912), who emphasises the important fact that the branches of the bronchi in the lung never end in culs-de-sac, but are all in inter-communication, forming circuits which can be traversed by pure air, from one end or the other, according as the air comes from the air-sacs or from the trachea. The lung thus consists of a labyrinth of air-containing branches inter-penetrated by a labyrinth of blood-capillaries. Every blood capillary is surrounded on all sides by air. Thus the bird's lung has a structure very different from that of the mammal's lung.

The joining of one bronchial branch with another is important ; it leads to the formation of " bronchial circuits," making the lung like a labyrinth. According to W. A. Locy and O. Larsell (1916), much importance should be attached to the " recurrent bronchi," recognised by Schulze and Juillet, which spring from the air-sacs and grow back into the lungs, where they establish numerous connections with the bronchial branches. So that the air-sacs are not to be thought of altogether, at least, as terminal sacs ; they may also be regarded as expanded reservoirs on the course of the bronchial circuits.

There are several points of great interest in regard to the development of the bird's lung. Like every other lung it arises as a ventral pouch from the anterior end of the food-canal, and is therefore lined by endoderm. But as it grows out from the food-canal it carries with it an ensheathment of mesoderm, which is most strongly developed on the ventral aspect of the lung, exposed to the body-cavity. To put it more precisely, according to the researches of W. A. Locy and Olof Larsell (1916), the endodermic pouch lies in a layer of mesenchyme that is bordered on the surface towards the body-cavity by a well-defined layer of

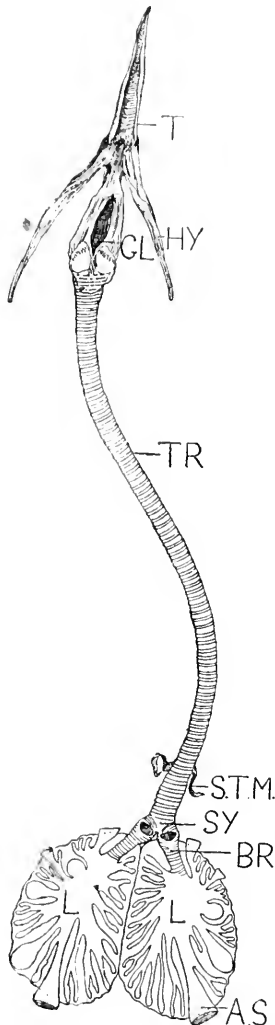


FIG. 34.—Windpipe and lungs of bird. T., tongue; HY., horns of hyoid; GL., glottis; TR., trachea; S.T.M., sterno-tracheal muscles attached to breastbone; SY., syrinx; BR., bronchial tubes; L., cavity of lung; AS., meso-bronchus leading into the abdominal air-sac.

mesothelium. Now the endoderm of the pouch gives off numerous hollow buds in a complicated way and these form the "bronchial tree" of the lung. They branch and branch, but the image of a tree is inaccurate since the branches unite by a network of inter-communicating passages. Eventually in the fully-developed lung no bronchial twigs end blindly. Of the complicated internal configuration of the endodermic lining which forms something like an irregular labyrinth, the mesodermic envelope of the lung gives no indication whatsoever.

To sum up, the special adaptations of the bird's respiratory system are—(1) the large internal surface of the lungs, due to the complex branching of the bronchi; (2) the great development of air-sacs which increase the efficiency of the lungs; (3) the fixing of the lungs to the ribs so that the movements of these in flight helps the expulsion and inrush of air.

§ 6. EXCRETION

All vital activity seems to involve—whatever else it involves—the metabolism of proteins, namely, the nitrogenous carbon-compounds which are invariably present in living matter. Take albumin as a sample. Every cell

is a laboratory ; the furnishings of the laboratory are made of proteins ; as the everyday operations go on there is wear and tear of these ; and thus there *must* arise *nitrogenous waste-products*. These are poisonous, auto-intoxicant, fatiguing—and they must be got rid of, which is the function of excretion.

But this is not the whole story. All animals eat protein food ; and very generally, too much of it. The chemical energy of this food-material makes it practicable for the protein-organisation of the animal to make a stir in the world. Proteins mean munitions ; and, although plants make the bulk of them (though not the best of them), plants have hardly learned to use them.

The proteins of the food are changed by digestive ferments into amino-acids which are distributed by the blood. These serve in small part as material for growth and for the repair of the protein framework in the cells of the body. But in great part the amino-acids are chemically changed to form hydrocarbon acids which are burnt within the body to supply energy. This chemical change takes place mainly in the liver, and it is associated with the formation of ammonia. This goes to form urea in mammals, and this is filtered out by the kidneys. In birds, the result of the kidney's filtration is a clear liquid in the duct (or ureter) which carries it away ; but this duct opens into the cloaca (the dilated end of the food-canal, occurring, for instance, in reptiles, birds, and the three egg-laying mammals), and the filtrate is delayed there. In the bird the walls of the cloaca appear to absorb water from the filtrate, which thus becomes semi-solid, and consists mainly of urates or salts of urea.

We see then that the nitrogenous waste-products of the bird's body are partly due to the wear and tear of the protein framework of the cells, and partly to the nitrogenous residue of the food-proteins which are burnt away as a source of energy. In the same way, in an engine we might distinguish fine particles of steel, due to the actual wear and tear of the machinery, from the ashes which resulted from unused fragments of the fuel.

The two kidneys of birds are three-lobed red organs, which lie embedded underneath the hip-girdle. They receive their blood mainly from renal arteries and they return it to renal veins. These join the great posterior vein, the inferior vena cava, leading back to the heart.

§ 7. THE USES OF THE BLOOD

The blood permeates the whole body, carried from the heart by arteries, carried back to the heart by veins. Fine branches of the arteries—arterial capillaries—become connected with fine tributaries of the veins—venous capillaries, so that the blood circulates in a continuous system. There is diffusion from the blood into the tissues traversed, and the tissues are even more directly bathed by the lymph fluid which moves in channels and vessels, the latter eventually communicating with the venous system. The blood is a common medium for the whole body, from which all parts take, and to which all parts give. It is more to the body than the Nile to Egypt.

Let us inquire, then, what the bird's blood is and what its uses are.

The blood consists of a complex fluid or serum in which there float red blood-cells and colourless blood-cells. The former, the erythrocytes, are nucleated cells or corpuscles, elliptical in outline, and slightly biconvex; thus differing markedly from our own, which are non-nucleated, circular in outline, and slightly biconcave. The members of the camel family are the only mammals where the red blood corpuscles have the elliptical shape seen in birds and reptiles, amphibians and fishes. As to the white blood corpuscles or leucocytes, they are nucleated amœboid cells, often changing their shape, and there are several different varieties. Among these kinds are the phagocytes, which are prone to leave the blood and migrate in the tissues, engulfing microbes, devouring degenerating tissue, transporting material from one area to another, and helping to repair injuries. They form a body-guard against invading bacteria; whenever there is inflammation they are

at work. Metschnikoff found some which were transporting pigment from a feather, and others which were eating away at the brain of an over-aged parrot—eating away at part of the body to which they themselves belonged.

The bird's red blood corpuscles are elliptical slightly biconvex discs, gradually pointed at the ends. According to Venzlaff (1911), they vary in number from 1,715,000 to 5,400,000 per cubic centimetre, tending to be more numerous when they are small. For man the number is about 5,000,000 per cubic centimetre, and 4,500,000 for woman. They arise in part from the cells in the medulla inside the bones and in part from the spleen. There is considerable diversity in the dimensions of the red-blood corpuscles in birds, even in the same species. A common size, according to Magnan (1911), is 13.3μ by 6.5μ . Some of the large birds of prey have distinctly larger corpuscles, e.g. 17.7μ by 8μ in the vulture (*Gyps fulvus*), but there does not seem to be any general correlation between size of bird and size of corpuscle. For comparison we may quote a few measurements of the diameters of mammalian red blood corpuscles—elephant, 9.5μ ; man, 7.5μ ; dog, 7μ ; horse, 6.5μ ; ox, 5.5μ ; Javanese chevrotain, 2μ . It is plain that the red blood corpuscles of birds are on the whole larger than those of mammals, but the difference of shape must be borne in mind. By μ is meant a micron, *i.e.* one thousandth of a millimetre.

The blood of birds may be called the richest blood in the animal kingdom, for it seems to have more red blood corpuscles per ounce than in any other animal. This corresponds to the intensity of their life and to their aerial activities. People who go to live at high altitudes acquire perhaps 20 per cent. more red blood corpuscles—an adjustment to the increased difficulty of breathing which follows from a decrease in the percentage of oxygen in the atmosphere.

The cells of the blood float in a serum—a complex mixture of salts, dissolved food-materials, and fluid nitrogenous waste. Biologically considered, the salts are

interesting in their close correspondence, in nature and in proportions, with the salts of the sea. This is surely a hint that blood-containing animals began their evolution in the sea. Birds sprang from reptiles, these from amphibians, and these from fishes, which bring us to the sea. The difference in proportion between the salts in the sea and the salts in the blood of a higher animal is lessened when we take into account the change that has occurred in the composition of sea-water since the time of the primeval ocean when blood was first established.

The chief uses of the blood are five :—

(1) The blood is a gas carrier. It carries oxygen from the place of capture (the bird's lungs) to the place of combustion (the muscles and other tissues). The oxygen is mainly carried by the red blood corpuscles, whose pigment hæmoglobin enters readily into a loose union with oxygen. But the blood also carries carbon dioxide from the place of production (the muscles and any other active tissue) to the place of elimination (the lungs). The carbon dioxide is mainly carried by the serum of the blood, *e.g.* in union with sodium salts.

(2) The blood carries and distributes the digested proteins (changed into peptones, etc.) and the digested carbohydrates (changed into sugar). These products of digestion are absorbed from the walls of the stomach and intestine, and after passing through the liver are distributed through the whole body. The digested fat (changed into fatty acids and glycerol) is first collected by the lymphatic system, which eventually communicates with the veins and the general circulation.

(3) With the help of the lymph the blood collects the soluble nitrogenous waste-products of the body, and these are eliminated by processes beginning in the liver and completed in the kidneys.

(4) The blood also distributes through the body the potent internal secretions of the ductless glands, such as the thyroid and the supra-renal. These will be discussed in a subsequent paragraph.

(5) The blood also contains the phagocytes whose various functions we have already referred to, and by means of these or other kinds of white blood corpuscles it is able to produce within itself subtle counteractives or "anti-bodies" which are able to antagonise poisons.

The bird has a first-class, four-chambered heart, with a complete separation of venous and arterial blood, just as in mammals. There is but a slight imperfection in the valvular arrangements between the right auricle (receiving all the impure blood from the body) and the right ventricle (driving the impure blood to the lungs); but perhaps too much has been made of this. For it is surely a relatively trivial evolutionary detail—this imperfection in the right auriculo-ventricular valve of the bird's heart. Its greatest interest, perhaps, is that we find collateral echoes of it in the heart of the egg-laying Duckmole—a primitive mammal.

The origin of the blood-cells in the individual bird is a question too difficult for this book. It seems that the original stock arises in various centres where mesoderm-cells proliferate. These "blood-cradles" or "hæmatopoietic tissues" may occur in various parts of the body; leucocytes may be produced in the bursa Fabricii; leucocytes and erythrocytes both arise in the marrow of the bones and in the spleen. But there is a special difficulty in the question where the multitude of red blood corpuscles in bird's blood has its origin. For in many birds the marrow of the bones is used up very early. It is believed by many, though the evidence is insecure, that the worn-out red blood corpuscles are destroyed and fresh white blood corpuscles are produced in the spleen of mammals. This may be so in birds also.

The spleen has been removed from mammals without appreciable effects on the health. It is possible that in birds it is more essential, and that it is a "cradle" of new red blood corpuscles, as well as a destructor of those that are worn-out and effete. *But we do not know.* A large number of measurements made by Magnan and De la Ribosière (1911) yielded the curious result that large birds

have a relatively smaller and lighter spleen, and smaller birds a relatively larger and heavier one.

§ 8. WARM-BLOODEDNESS

This is an awkward word for a very important quality, namely, that of keeping up a practically constant body-temperature. It means that there are arrangements for keeping a balance between loss of heat and production of heat, and the only warm-blooded animals are birds and mammals. They are technically called stenothermal (of constant temperature) in contrast to reptiles, amphibians, and fishes which are poikilothermal (of changeable temperature)—in plain English, “cold-blooded.” But this is just a case where the “plain English” is not very useful. If we say that a snake is a “cold-blooded” animal, this surely suggests that it must have a low temperature; but that cannot be true of a snake basking in the sun in the Sahara. “Cold-blooded” means tending to approximate to the temperature of the surroundings; “warm-blooded” means keeping the same body-temperature, day and night, year in year out. We repeat that birds and mammals are the only warm-blooded animals; and the fact that birds have a body-temperature 2° – 14° F. higher than that of mammals does *not* make them any *more* warm-blooded.

There are many oxidations going on in the body which result in the production of heat, but the chief source is in connection with the contraction of the muscles—which goes on to some extent even when the animal is at rest or asleep. Every one knows that the body becomes cold more rapidly during sleep and that is mainly because most of the muscles are at rest. The regulation of the heat-production and the heat-loss is due to the activity of a nerve-centre in the corpus striatum of the cerebral hemispheres. It is called the thermotaxic centre, and it is sensitive to the temperature of the blood and probably to messages from the skin. When the temperature is lower than usual, the centre sends out orders to the muscles, commanding them, as it were,

to produce more heat. These orders may follow on the heels of one another very quickly, and the muscles may pass into an irregular sort of contraction, familiar in shivering. But the shivering is also associated with a constriction of the blood-vessels in the skin, for the heat-regulating centre also sends messages to the periphery. If the blood-vessels in the skin contract, there is less loss of heat from the skin. If the regulating centre should be warmed by the blood, it sends out orders which bring about muscular relaxation and therefore less production of heat. And it also brings about dilatation of the blood-vessels in the skin which increases the loss of heat. In mammals the warmth of the body is also reduced by sweating, but birds do not sweat. There may be an approach to "internal perspiration" in the diffusion of water-vapour into the air-sacs.

We see, then, that the temperature of the body can be regulated by increasing or decreasing the production and also the loss of the animal heat. The importance of the animal heat is that it enables the chemical reactions in the body to go on more rapidly and smoothly.

All birds are warm-blooded as adults, but in the young birds the thermotaxic arrangements have not been completed, and the danger of over-heating or over-cooling is great. The very young bird is in this respect not far from a reptile.

§ 9. THE REGULATORY SYSTEM AND THE RESULTING CORRELATION

There are a number of organs in birds that were till recently great puzzles, for physiologists had no clear idea of their use. These are (1) the paired thyroids lying at the base of the neck, arising in development as a pouch from the food-canal, but ceasing to have any connection with anything save blood-vessels; (2) small yellowish suprarenal bodies lying on the front part of the kidneys, and having a very complex development, partly in connection with the embryonic kidney and partly in connection with the sympathetic nervous system; and (3) a pituitary body, a

remarkable organ, partly nervous and partly glandular, which hangs down from the floor of the optic thalami of the brain, and arises in development as a downgrowth from the brain meeting an upgrowth from the mouth, the two portions entering into very intimate union.

All these organs are secretory and all are ductless; they are known as organs of internal secretion or endocrinal glands. The fluid substances they produce are carried away by the blood and distributed throughout the body, having specific effects upon specific parts. There are some other parts of the body which produce internal secretions which the blood sweeps away. This is true, for instance, of the reproductive organs (ovary and testis), though their primary and chief function is, of course, to make ova and spermatozoa. The exceedingly important uses of the internal secretions must now be considered.

There is undoubtedly a certain amount of competition among the different parts of the body, but the larger fact is their correlation. They seem to work into one another's hands, as if they had, in St. Paul's words, "a common concern for one another." This harmonious unification is in great part due to the nervous system, which has what one of the great neurologists calls an "integrative function." The central government is made aware of the needs of the outlying parts, and may supply these almost automatically, reflexly, as we say. More than that, the remote parts and the intricate recesses may be thrilled by or attuned to the purpose and feeling of the central government. "An artist to his finger-tips," we justly say. Another correlation is effected by means of the blood, that common medium from which every part derives sustenance and to which every part makes contributions. Now it is to the general idea of the blood as a correlating medium that there has been added in the last thirty years or so a recognition of the rôle of the ductless glands or "organs of internal secretion." Apart from anticipatory glimpses by Claude Bernard and others, it is to Brown-Séguard that credit is due for first clearly discerning that a specific secretion may

be contributed to the blood by a particular organ and distributed through the body with very effective results, especially in certain parts. The word "hormone," which means excitant, was invented by Mr. W. B. Hardy in connection with the remarkable discovery of "secretin" by Professors Bayliss and Starling in 1902. This substance "secretin" is produced in the presence of acid by the cells lining the beginning of the small intestine; it is carried away by the blood-stream and it excites the pancreas or sweetbread to secrete its very important digestive juice which is poured into the food-canal. Thus, when a meal is in process, or it may be in prospect, there is by means of the excitant secretin a preparation for its digestion, and this illustrates what is meant by physiological co-ordination or correlation. For it is plain that the beginning of the intestine and the sweetbread work into one another's hands. Although the word hormone really means excitant or stirrer-up, a wider idea was from the first associated with it, namely, that of "chemical messenger"; as Sir Edward Schafer points out, it might have been happier to have thought of the messenger of the gods and made the word not "hormone" but "hermone." But this is being wise after the event, and although there are hormones which inhibit instead of exciting, the word has come to stay. The internal secretion by which ductless glands and specialised patches of tissue produce hormones is conveniently defined as follows by Professor Swale Vincent: "The process consists in the preparation and setting free of certain substances of physiological utility (the raw materials for which are supplied by the circulating blood) by certain cells of a glandular type; the substances set free are not passed out on to a free surface, but into the blood-stream." It is not too much to say that the discovery of the *rôle* of hormones has changed the whole face of physiology. It has also added incalculably to the biological control of life.

It may be that even in plants there are analogues of hormones, chemical messengers by which one part can influence another at a distance; and it may be that future

discoveries (the inquiry is still young) will show that hormones are important in backboneless animals, where as yet we have only hints of their presence ; the actual fact to-day is that it is only in regard to backboned animals that we are sure that hormones play an indispensable *rôle* in the internal economy of the body. It should be remembered that in backboned animals the blood comes to its own in a way that does not hold true for the lower reaches of the animal kingdom. The hormones in regard to which physiologists have securest knowledge are those produced by the thyroid gland, the parathyroids, the suprarenal bodies, the pituitary body, the mucous membrane of part of the digestive tract, certain islands of tissue in the sweetbread or pancreas, and the reproductive organs. It is obvious from this list that hormones are formed in very diverse parts of the body, and this suggests the further fact that they have very varied properties.

(1) Deficiency in the activity of the thyroid gland which lies on each side of our larynx spells arrest of development, cretinism, goitre, and the like ; and every one knows of the modern miracle by which these abnormal states are counteracted by giving the patients injections of the extract of the thyroid gland of sheep. An exaggeration of the activity of the thyroid leads to exophthalmic goitre and other disorders, for excess is as dangerous as deficiency. In a general way it may be said that the hormone of the thyroid seems to regulate the metabolism of the body, especially affecting the nutrition of connective and nervous tissues. It tends to keep the activity of nerve-cells up to the mark.

(2) Of the smaller parathyroids, which are associated with the thyroid, it may be safe to say, although the hormone has not been isolated, that they put a brake on the excitability of nerve-cells. In other words, their internal secretion is, in Sir Edward Schafer's terminology, a chalone rather than a hormone. But both would be included in Professor Starling's definition : " By the term ' hormone,' I understand any substance normally produced in the cells of some

part of the body, and carried by the blood to distant parts, which it affects for the good of the organism as a whole."

(3) The adrenalin produced by the medullary part of the suprarenal bodies (situated in front of each of the kidneys) is a very potent hormone, whose secretion is greatly increased by strong emotion, *e.g.* of fear or rage. It brings about a rapid increase in blood pressure, it affects the distribution of the blood and the breathing movements, it increases the excitability of the skeletal muscles and their power of resisting fatigue, it increases the amount of sugar in the blood and its coagulability. It is easy to see that when the emotion of rage stimulates the flow of adrenalin, it thereby prepares the body for a fight in a somewhat detailed and very effective physiological fashion. Similarly, the useful effect of adrenalin in contracting the tiny muscles that erect the hairs of the skin is familiarly illustrated when a frightened or at any rate excited cat increases its size in facing up to a dog. Adrenalin is interesting in being the only true hormone which has been made artificially; yet how far it is from being a simple substance is suggested by its chemical name ortho-dioxyphenol-ethanol-methylamine, which surely means some labour of synthesis whether in the chemical laboratory or in the alchemy of the living cell.

(4) Over-activity of the pituitary body, which projects from the under surface of our brain into a well-protected bony cup about the size of a small hazel-nut, leads to the development of an unhealthy giant; pituitary insufficiency leads to an unhealthy dwarf, slow of pulse and weak in energy. Both of these extremes are to be distinguished entirely from healthy giants and dwarfs, who arise as freaks or mutations. But besides regulating growth, the pituitary body (especially in its posterior lobe) has to do with the storage and mobilisation of carbohydrates.

We see, then, the variety of the functions which hormones discharge, and the impression would be heightened if we considered those produced by certain parts of the wall of the alimentary canal; or that produced by peculiar islets in the pancreas, which have to do with carbohydrats

metabolism ; or those proceeding from the reproductive organs which have to do with the development or non-development of secondary sex-characters, or with the preparation of the mother for the child both before and after birth. The complexity of the situation is increased by the fact that one organ of internal secretion may produce more than one hormone, and that there may be reciprocal inter-relations between glands, so that they corroborate or counteract one another. It is difficult to answer the question : What, if anything, is the common characteristic of hormones ? They vary greatly in chemical composition ; they have specific effects, but except when a structural result ensues these effects do not last unless more hormone is produced. They are not ferments, yet they operate in minimal quantities. Perhaps their only common characteristic is the negative one, that they never evoke antibodies or counteractives, as many substances do when introduced into the blood.

To the evolutionist there is much about hormones that is interesting. (a) One type of animal sometimes differs from another in the length of different areas on its life-curve, one having a long-drawn-out senescence, and another a telescoped juvenility ; and we can see, as Professor Arthur Dendy points out, how this might be fixed in the course of ages by variations in the activity of the ductless glands at different periods of life. (b) It has been shown that a strengthening of the musculature of the legs, *e.g.* in mountain-climbing or in dancing, may be correlated with an increase in the strength of the muscles of the arms. This probably means that some chemical messenger, exciting to the formation of muscle substance, is distributed throughout the system by the blood. And this, as has been suggested by Mr. J. T. Cunningham and others, opens up the possibility that specific hormones produced in the establishment of individual modifications as the direct result of peculiarities of function and environment, might affect the reproductive elements in a representative manner, and thus likewise affect succeeding generations. (c) As to the

evolution of the hormones themselves we cannot go far, but we must think of the body as a vast system of symbiotic organs, tissues, and cells. There is a continual "pooling" of products, and there has doubtless been an age-long elimination of those parts whose contributions tended to endanger harmony and stability. It is probable that some at least of the hormones are end-products or by-products of a routine of metabolism which had previously some less recondite significance, and it is noteworthy that some of the hormones are produced by structures (*e.g.* thyroid and pituitary) which have drifted from their primary utilisation. It may be as Professor Starling suggests, that these end-product or by-product hormones have been retained in the course of evolution not so much because of any intrinsic philtre-like virtue in themselves, but rather because certain other structures happen to be peculiarly sensitive to their influence in the way of either spur or bridle.

CHAPTER VII

ADAPTATION TO HAUNTS

- § 1. Arboreal Life. § 2. Aquatic Life. § 3. Adaptations to Swamps.
§ 4. Adaptations to Desert and Steppe. § 5. Mountain Birds.
§ 6. Moorland Birds. § 7. Birds of the Sea Cliffs. § 8. Birds in
other Haunts. § 9. Protective Coloration.

LIVING, as Professor Geddes has remarked, is a continual adjustment between the Organism acting or functioning on its environment, and the Environment acting on the organism: $\frac{O-f-e}{E-f-o}$. As the direct, or, more probably, indirect result of the twofold process there have evolved permanent adaptations of the organism to its environment. In this chapter we have been particularly indebted to Dr. Hilzheimer (1913).

§ 1. ARBOREAL LIFE

It is highly probable that primitive birds were arboreal; it is certain that many birds of to-day have that habitat. A common arboreal adaptation is to have strong sharp claws on the toes, as in the Tree-Creeper which runs up the tree-stem in a spiral, helped in some measure by its stiff-pointed tail-feathers. By an alternation of jumps and grips the nearly related Wall-Creeper ascends a vertical cliff-face, catching spiders as it goes. Much curved claws are better suited for firm gripping than for rapid climbing, and the relative position of the toes, *e.g.* two forwards and two backwards in woodpeckers, may make the grip still better. The stiffening of the terminal part of the shaft of some of the tail feathers is seen in woodpeckers and some

parrots, and the way in which parrots may hang themselves up by their strong curved bills is familiar. Hilzheimer points out that the Grey-headed Parrot and the Woodpecker press their stiff tail against the branch even when they are climbing along underneath it with their back to the ground, and suggests that it has a directive rudder function, perhaps connected with the marked shortening of the legs in climbing birds. We see, then, that adaptation to climbing may affect the claws, the toes, the beak, and the tail.

§ 2. AQUATIC LIFE

Many birds that are not aquatic can swim, as has been observed in pigeons and quails, the buoyancy of the body doubtless helping; and the dipper or water-ouzel, which swims with its wings against the stream or walks along the bed of the river gripping the stones with its toes, is a notable instance of what a creature can do in the way of mastering a new medium without having any special adaptation thereto. For the dipper might almost be called an aquatic wren.

Yet there are many consummate adaptations facilitating aquatic life. (*a*) The legs are often very far back, as in diver, grebe, and puffin, sometimes so far back that terrestrial progression is difficult. Thus the penguins tumble down on all fours on the snow, and toboggan along using both "wings" and feet. The far back position of the legs enables the aquatic bird to strike backwards behind the body with little waste of power. The position recalls the propeller of a steamship or sculling from the stern of a boat.

(*b*) Very familiar is the utility of the webbed foot, a simple adaptation appearing first in frogs. But it is interesting to notice how it occurs in birds which are but distantly related to one another. Thus the Storm Petrel is not related to the Gull Tribe, nor the Puffin to the Penguin, nor the Duck to the Diver, though all are web-footed. The adaptation of the web-foot is not restricted to affording a continuous and resistant surface for striking the water;

in most cases it folds together neatly in being drawn forwards for the next stroke, thus reducing the friction. In some cases, as in divers, the tarso-metatarsus region before the toes begin is laterally compressed like a knife blade. When the leg strikes quickly backwards, all the force is concentrated in the webbed foot, the blade of the oar as it were; and when the leg is drawn forward for the next stroke the sharp edge of the tarso-metatarsus and the collapse of the webbed foot must reduce the friction greatly. In ordinary cases the feet are used alternately, but many may have noticed how an excited swan will kick violently backwards in the water with both feet at once.

(c) The water-ouzel or dipper uses its wings as organs for swimming under water, and they do not show any notable transformation. The Diving Petrel swims deeply with its wings and emerges *flying* from the surface of the sea. A similar use of the wings as organs for under-water swimming is seen in various members of the auk family, where the wing is long, narrow, and pointed. In the flightless Great Auk the wing had no use except in the water.

A storm-petrel, diver, puffin, little auk, or any similar bird, moving on the surface of the sea is obviously swimming by means of its feet only. But the very reverse is to be seen in the penguins, where the hind legs are stretched out behind as a rudder, but the transformed wings are powerful paddles. They are flipper-like and relatively short, covered with flat reduced feathers, and move en bloc except at the elbow joint. The bones are greatly compressed laterally and their detailed shapes tend to restrict the possibility of their moving on one another, except at the elbow where a restricted mobility admits of a somewhat screw-like twisting. The musculature of this strangely transformed wing is reduced to a vanishing point, but there are strong sinews which bind the bones tightly together. No bird that has a functional fore-limb at all shows such a transformation as the penguin, and yet it is important to observe how little the essential architecture has been departed from. Hilzheimer notes that the fossil penguins of Seymour Island

are less divergent from the ordinary Carinate type as regards both fore and hind limbs.

It is instructive to take a particular case in more detail—puffins, for instance. These attractive birds have short, narrow wings, but their flight is rapid and often zigzag, that is to say, under rapid control. When they launch themselves from a cliff, head bent down, wings raised up, webbed feet spread out behind, they often describe a fine whirring sweep before they alight with a splash in the sea. They paddle

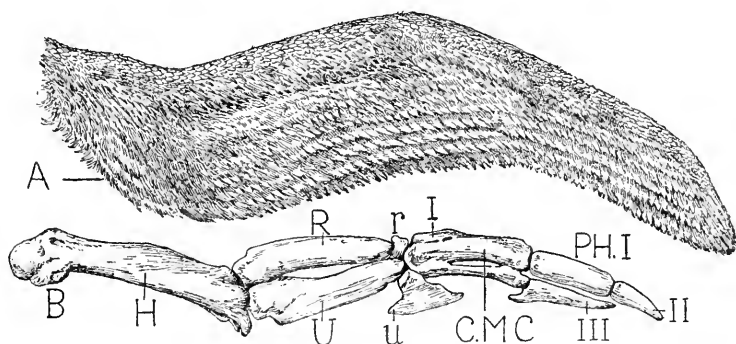


FIG. 35.—Wing of Adélie Penguin, *Pygoscelis adeliae*. A., from a specimen; B., after Pycraft. A novel structure, a flipper, has arisen from a typical wing, without very radical transformations. H., humerus; R., radius; U., ulna; r., radiale; u., ulnare; CMC., carpometacarpus; I., the thumb; PH.I., the first joint of the first finger; II., the second joint; III., the second finger or third digit.

deftly on the surface with their feet, but they swim underneath the water with their wings. Indeed, it may almost be said that they fly under water. Unless helped by a head wind, they find it difficult to rise into the air, and they often splash along for some distance before they are clearly launched in flight. But they often fly several miles to the fishing ground many times in a day. Sometimes a large flock may be seen wheeling in unison, recalling the fact that auks (the family to which puffins belong) are related to the gregarious plovers. To this repertory of movements there has to be added the burrowing, for the nest is often at the end of a yard long tunnel. In the tunnelling, which is said

to be mainly the male's work, the bird uses its laterally compressed bill or "coultter-neb" and also its feet which, though webbed, bear strong nails.

It is a great pleasure to watch the movements of a Little Grebe or Dabchick on a quiet reach of the river. Rising upright out of the water, it turns a somersault so quickly that our eye cannot follow what happens. It dives head foremost and reappears *somewhere else*. It is always doing this, "quicker than a shot," for it feeds usually on very small animals, and it takes many a pickle to make a mickle. Under water, it can use its wings as well as its chestnut-leaf feet. It is a very quiet creature, elusive to a degree, with an extraordinary power of self-effacement. Without any splash it seems able to submerge itself, we do not know how. And the training of the young birds by the mother is most admirable.

(d) Adaptations of plumage to aquatic life may be well illustrated by the thick soft covering on the under surface, reaching a climax in grebes. The feathers are concave towards the body, they overlap those behind them, they are well greased, they include much air in their capillary spaces; nothing could be better adapted to conserve the precious animal heat in the cold water. Moreover, beneath the skin in which they are implanted there is a thick layer of fat.

In many of the ducks and geese (Anseriformes) the contour feathers on the underside below the wing are disposed, as Heinroth has described in detail, almost at right angles to the long axis of the body, so that they form a sort of pocket for the wings. This is important, for it prevents the wings from becoming wetted; and it is interesting to notice that the development of the pocket is more perfect in the Diving Ducks, which have not to keep flapping their wings dry as non-diving ducks do. It is very interesting, as Hiltzheimer points out, that birds like cormorants which only enter the water occasionally have to spend a good deal of time drying their wings when ashore, whereas more thoroughly aquatic birds, which remain

habitually on or under the water, like the Diving Ducks referred to, have the pocket of feathers well developed, which keeps the wings dry. Such is adaptation !

The preening of the feather, so familiar in ducks, probably serves to keep the plumage dry. A thick layer of subcutaneous fat serves like the blubber of whales to conserve the animal heat. The air-spaces under the skin of some aquatic birds, like the solan goose, may increase the non-conducting quality.

§ 3. ADAPTATIONS TO SWAMPS

The long legs of many of the waders, such as redshanks and greenshanks, enable them to go relatively far into the water, in search of food, without getting wetted. The foot of the stork, with the three anterior toes slightly webbed, and the backward-turned first toe well-developed, is as well suited for following the frogs as are its stilt-like legs. What is seen hinted at in the long toes of the water-hen reaches its full expression in the South American Jacana, whose very long four toes with equally exaggerated claws are admirably adapted for walking on the surface of floating water-leaves.

§ 4. ADAPTATIONS TO DESERT AND STEPPE

Hilzheimer notes that it is advantageous to lessen the surface of contact if there is to be swift running over the desert ; so the backward-turned toe tends to disappear, and the African Ostrich has only two toes. Moreover, as in the camel, there is in the Ostrich a soft elastic cushion underneath each toe, which prevents sinking into soft sand. The ostrich, with its great stride of six feet, is a diagrammatic instance of the very long legs that desert birds often have. A notable exception is seen in the sand-grouse, where the legs are unusually short. Hilzheimer explains this by referring to the powerful flight of these birds. The sand-grouse (*Pterocles*) has the three anterior toes united by

membrane up to the claws, and the resulting broad foot is well adapted for running on soft snow or sand. When the sand-grouse half-bury themselves in the steppe they are practically invisible, so well does their dorsal plumage harmonise with the surroundings. In Pallas's sand-grouse (*Syrrhaptes*) the broad toes are bound together in a web, with a warty sole beneath. In the cold Tibetan steppes the upper surface of the whole foot may be covered with small feathers, and in the ptarmigan, which spends the winter among the snow, there are feathers on the under surface of the foot as well as on the upper.

§ 5. MOUNTAIN BIRDS

A simple functional adaptation is seen in the heart of the ptarmigan which lives at high altitudes where breathing is more difficult owing to the rarer air. This implies that the blood must be sent to the lungs more frequently. Strohl has found (1910) that the right ventricle of the ptarmigan is noticeably stronger than it is in the nearly related willow-grouse which lives at lower levels. Even the young ptarmigan shows the hypertrophy.

The ptarmigan shows another adaptation in its change of colour. For the brown and grey plumage of summer and autumn, which makes the bird inconspicuous against such background as lichen-covered rock, is replaced in winter by a white suit. This not only gives the ptarmigan a garment of invisibility against a background of snow, thus saving it from the eagle's eye, but it is physiologically the most economical dress for a warm-blooded animal, with a high temperature, in very cold surroundings.

An interesting adaptation in the American Ruffed Grouse (*Bonasa umbellata*) is described by Austin Hobart Clark (1910). When winter sets in there is a development of "snow-shoes" formed from a row of scutes on each side of each toe. This increases the superficial area of the bird's foot by as much again. "Thus a bird walking about in the winter brings to bear only half as much weight on any

PLATE IV



[Photo by Kattar, Lerwick.

EGGS OF RINGED PLOVER (*F. galeata*)

They are laid in a depression among the shingle paved by small stones and broken shell. They are yellowish and brown-spotted, very inconspicuous.



[Photo by Norrie, Fraserburgh.

YOUNG HERRING GULLS (*Larus argentatus*).

The mottled plumage makes them very inconspicuous.

given spot as the same bird in summer, and is thereby enabled to tread securely upon slightly compacted snow." These snow-shoes recall the scolloped margins of the toes in a grebe, where, however, the adaptation has reference to increase of the surface which strikes the water in swimming. In the same Ruffed Grouse there is an interesting habit-adaptation in the winter, when it dives or tunnels into the loose snow of drifts, having discovered its value as a non-conductor. It may make a tunnel about two feet long, and lie in retreat for several days. Complete burrowing is also reported in the case of the British Red Grouse.

There are many "birds of the mountains," like chough and Alpine swift, which get on well at high altitudes without showing any special adaptation. They have found a niche of opportunity which they utilise, for part of the year at least, with great success. A good example is the beautiful Wall Creeper (*Tichodroma muraria*), seen on the High Alps in summer and on the shore of Lake Geneva in the winter. It comes fluttering down beside a precipitous cliff, circling in the air like some dark moth, and then it begins to jerk itself up the surface of the rock, like a brilliant butterfly with crimson and yellow. It grips with its toes and with its long slender bill it captures small spiders and insects from the crevices. It makes its nest in some inaccessible cleft and is very careful in its coming and going. For the summer it has conquered the mountain-side, but we do not know that it shows any special adaptation to the high altitudes.

Biological Classification of Mountain Birds.—We wish to suggest a classification of the birds (and the mammals) of the mountains into three contingents—the *relicts*, the *insurgent colonists*, and the *refugees*.

By the *relicts* we mean the survivors of an Arctic or tundra fauna of *resident* birds, which in Glacial Periods extended far into Central Europe. When the climate became milder and the glaciers retreated, some of the northern birds went further north again, others became migratory, others were eliminated, and others *went up the*

mountains. Those that followed the last alternative are the relicts, and a good example is the ptarmigan. It is a distinctively northern bird, and in the more southerly part of its range it is confined to high altitudes. In Scotland it has disappeared from the southern counties. On the Cairngorms and other Highland mountains it keeps its foothold—a *non-migratory relict*. It can thrive on berries and shoots; it has a strong heart; it turns white in winter; and perhaps there is a touch of perfection in the way it moults its worn claws and finds fresh ones ready underneath.

The second contingent of mountain birds consists of insurgent colonists from the crowded low grounds. Just as the industrious Swiss migrate in the summer to their "alps," and feed an astonishing number of cattle on these high mountain-shelves, so many birds and mammals have colonised the heights, but more permanently. As an instance we would cite the Golden Eagle. On the whole, it seems justifiable to regard it as a colonist of the heights, that has followed in the track of such palatable creatures as the grouse and the Mountain Hare. It is a slowly multiplying bird, in a high degree an aristocrat, somewhat of a specialist in its diet, and it has sought out a mountain-home of its own, where it can live dangerously and yet survive. Other examples of this contingent would be the rock-creeper, the rock-thrush, the Alpine swift, and the snow-finch.

The third set of mountain birds includes the refugees, hard-pressed creatures that have sought out an asylum—a way of escape from the too intense competition of the crowded low grounds. As an instance we may take the dipper or water-ouzel, a bird particularly fond of mountain-streams, going up as high as there is rippling water. The water-ouzel has a brilliant white breast, and it is often difficult to be sure whether we are looking at the bird or the foam of the water as it breaks over a stone. It is a near relative of the wrens, that has found its niche of opportunity in becoming aquatic and going high up. It walks on the

bed of the stream, gripping with its toes, and, as we have mentioned, it also uses its wings in a sort of under-water *flight*. It feeds on small water-animals, and makes a domed nest of grass and moss under a waterfall, or in some similarly safe place. The male's wren-like song may be heard in mid-winter, sounding so cheerily from a stone on the mountain stream that we wonder if the word conqueror would not have been more appropriate than refugee.

§ 6. MOORLAND BIRDS

Characteristic of the high moorland are such birds as curlew and whimbrel, stone-chat and whin-chat, golden plover and grouse. Let us take two types—the first and the last. The curlew owes part of its success to its varied diet ; it feeds in summer on insects, grubs, earthworms, slugs, juicy fruits like the crowberry ; in winter it frequents the seashore and picks up all sorts of small animals. It is a striking feature of the moorland during its courtship period in spring. As we have said in our *Mountain and Moorland*, “ the male bird soars to a considerable height in the air and hovers ; it sinks and rises again ; it circles and hovers again ; and all the time it pours forth for its desired mate's ear a simple, trilling song, certainly not plaintive, singing over and over again—‘ Courlee, courlee, courlee.’ ” This is very different from the melancholy “ Whaup, whaup ” of the winter season. The nest is simply a depression made comfortable with grass, and in it are laid the four large eggs, greenish and brownish, with their points towards the centre. The brooding bird sits very close, and the brown, streaked plumage often harmonises beautifully with the withered bracken and herbage round about. The bird has a garment of invisibility.

The Red Grouse is interesting in being a native of Great Britain and of no other country. Just as there is a St. Kilda wren, so there is *Lagopus scoticus*. This means that from a relatively generalised grouse-stock, from which ptarmigan and willow-grouse have sprung, there arose in Scotland

another variant which suited the moorland conditions and has become a species. Although it has been introduced elsewhere, as on upland heaths in the north of England, on many Welsh moors, and on many Irish hills, it flourishes best in Scotland, where, we believe, it was first evolved.

The Red Grouse is a resident bird, moving very little unless the winter is unusually severe. The Spartan diet, which its extraordinary digestive powers enable it to endure, accounts for its survival in an environment which would be fatal to most creatures of high degree. For it feeds on the tips of the twigs of ling and heath, crowberry and blaeberry, besides, in autumn, the seeds of sedges and grasses—very frugal fare. It seems that the young grouse require more digestible food than their parents demand, and there is said to be a definitely *insectivorous* period, during which the food-canal becomes educated for more difficult tasks.

The Red Grouse is full of biological interest. Thus the red warty ridge above the eye has the same pigment (*zoone-erythrin*) as in lobster and shrimp; the feet are stockinged in feathers that go as far as the ends of the toes; the worn claws are moulted off in late autumn, liberating a fresh set well-suited for the winter's scratching for food. There seems to be no specific "grouse-disease," but when the birds live a too sheltered life and constitutions below par are tolerated, then the parasites of the grouse—normally kept within bounds—get the upper hand and are fatal to their host.

§ 7. BIRDS OF THE SEA-CLIFFS

There is a very characteristic bird-fauna on sea-cliffs like those of Flamborough Head, the Bass Rock, Ailsa Craig, Handa Island, and Foula. There are some tenants which remain throughout the year, as in the case of cormorants and kittiwake gulls; in other cases the birds are there at the breeding season only, as in the case of guillemots and puffins. The permanent tenants of the cliff and the summer lodgers are there and not elsewhere because of the presence of endless

shelves and nooks on which the eggs can be laid. There may be tier upon tier for hundreds of feet, like a giant's bookcase.

Conspicuous among the summer visitors are the guillemots, dark slate grey or dark brown above, and brilliant white below. For a large part of the year they are rovers on the open sea ; it is only in spring and summer that they frequent the cliffs. They float buoyantly on the water or swim rapidly on the surface with their long webbed feet ; and under water they use their long narrow wings with great effect. They are not fond of flying on the open sea, but a sudden alarm will prompt them to take to wing, and they hurry spluttering over the waves. On the cliffs they shuffle about rather awkwardly, but this is mainly because of the difficulties of the situation. The whole of the instep (tarso-metatarsus) is horizontal, and that enables the guillemot to grip the rock when it alights and to scramble safely on very steep gradients. It is interesting to notice that this splay-footedness is secondary, for the young guillemot stands with its instep almost vertical, as in ordinary birds.

When spring comes the rovers return from the open sea to the cliffs, where they have been unrepresented all through the winter. Why should hundreds of thousands come together ? The answers are : (1) that guillemots are scions of a gregarious (plover) stock ; (2) that it is instinctive in migratory birds to return to the place of their birth ; and (3) that there is only a small number of suitably shelved sea-cliffs with good fishing in the vicinity.

As adaptive to the cliffs we have mentioned the horizontal instep, and we may add the top-like shape of the egg, which does not *roll* when jostled, the reduction of the clutch to one, which is held lengthwise underneath the body and in part lifted on to the long feet, and the sluggishness of the young bird which eats heavily and sleeps much on its dangerous cradle. Guillemots are monogamous, for the season at least, and there is on the crowded cliff some approach to conventions in human society. Thus there is, to begin with, keen competition for a shelf or niche, but a

guillemot does not interfere with its neighbour's egg or progeny.

Razorbills are near relatives of guillemots, but may be distinguished by the laterally compressed bill, with white line on it, and by the strong white line running from beak to eye. The plumage of the under parts is of the same brilliant white colour, but the dorsal parts are black with a greenish gloss, while the throat and foreneck show velvety-brown. From our biological standpoint it is interesting to contrast two nearly-related species, which might be called "second cousins," to see how individuality finds detailed expression along many lines. Both birds incubate a single egg for thirty days, but the variability in the external colouring of the razorbill's egg is distinctly less than in the case of the guillemot's. Moreover, the interior of a razorbill's eggshell held against the light is greenish, whereas it is yellowish-white in the case of all guillemots, except when the outside of the shell is blue-green. Both birds are monogamous, but they differ in their courtship ceremonial. In both types the young bird is fed on small fishes, but the guillemot carries one at a time lengthwise, while the razorbill carries several crosswise. Such is *specificity*.

Another bird of the cliffs is the puffin, belonging to the same auk family (Alcidæ) as the guillemots and the razorbills. It is a highly individualised bird, marked by the stocky form, short neck, orange-yellow legs, and large, laterally compressed bill, brilliant in scarlet, blue, orange, and white. When alert it stands bolt upright and look as if it were resting on its tail. But this is, of course, an illusion. It is only when it walks about or crouches for a spring that the puffin plants more than its toes on the ground. When it is resting at its ease its pose sinks from the upright to the horizontal.

Just as razorbills and guillemots are usually found on different sections of the cliff-face, so the puffins often keep to themselves, preferring the top of the cliff where there is some soil in which they can burrow; for a rough grass nest is made at the end of a tunnel which may be a yard long. As already noted, this is usually excavated, but a

rabbit's burrow may be utilised if it is suitable. The single egg, in marked contrast to that of the guillemot and razorbill, is typically of a dull white colour. The numbers of puffins are often to be reckoned in thousands, in spite of severe persecution. Thirty years ago Professor Newton estimated the tenants of one haunt in the Hebrides at three millions.

§ 8. BIRDS IN OTHER HAUNTS

We need not pursue the inquiry further, for all that we are aiming at in this book is a suggestion of points of view. In the first part of this chapter we gave examples of special adaptations to diverse types of environment, such as trees and the open sea—to mention two which are very far apart. In the later paragraphs we have been suggesting the study of birds in their more detailed haunts. Just as there are "plant associations" characteristic of the seashore, the marsh, the pond, the wood, the mountain-side, and other haunts, so there are "bird associations" which are well-defined, for part of the year at least, and we have instanced mountain birds, moorland birds, and sea-cliff birds.

There are obviously other associations. Thus there are marsh birds, like the bittern and the crane, and the fact that neither is any longer a breeding bird in Britain, where they once were common, suggests the general remark that the spread of agriculture and the involved draining operations must mean the dwindling of marsh birds. Apart from small birds like reed-warbler and marsh titmouse, for which a limited area suffices, the marsh birds of an agricultural country are bound to be eliminated, unless indeed it is a country of innumerable lakes. Perhaps it would not be unfair to call the heron a persistent marsh bird, for although "heronries" are usually on lofty trees, much of the feeding is on marshy ground. By lochs as well as by the riverside we watch these elegant birds, with their extraordinarily alert immobility, waiting for an eel or some other victim to come within striking range. For the breeding season the Black-headed Gulls may be justly called marsh birds, for they take full advantage of the treacherous swampy ground.

Another association includes the birds of the woods and forests, such as the capercaillie which became extinct in Scotland about 1762 (and long before that in England and Wales), but was re-introduced from Sweden in 1837 and has now a firm footing in many parts of Scotland. Its relative the blackcock may also be included as a woodland bird. More distinctive is the tree-creeper, already mentioned, which runs up the bark like a mouse. There is safety in its very rapid movements and inconspicuous coloration. Its slender curved bill is admirably adapted for picking small insects and spiders out of the crevices; the long curved claws grip the bark in the jerky spiral ascent; the stiff-pointed tail-feathers brace the bird up when it pauses to peck. As in every other case, we have to deal with a bundle of adaptations. The woodpecker is another typical member of the association.

The largest group is that of hedgerow and meadow birds. We think of such familiar examples as hedge-sparrow, blackbird, wren, and shrike in the hedgerow; or lark, meadow-pipit, corn-bunting, and whin-chat in the meadow. But it would not be difficult to multiply these by ten, if one does not take the words hedgerow and meadow too literally.

Another association is that of river and estuarine birds. We think of the dabchick and the water-wagtail, the coot and the water-hen, the kingfisher and the water-rail. On the lower reaches of the river, or on the flat shores of the estuary, there are gulls, terns, dunlins, redshanks, and more besides.

§ 9. PROTECTIVE COLORATION

The flying bird readily catches the eye as an opaque object in the air, but against their natural backgrounds most birds are inconspicuous. In ordinary cases there are only isolated points in the plumage that reflect the light brilliantly, and when there is great splendour, as in the peacock's tail, or in the cockatoo's plumage, or in kingfishers and humming-birds, there is usually some counter-

active quality. The bird may be small, or a rapid flier, or very clever, or social ; or it may show its brilliance only on occasions of sex-display. Almost always there is some quality or habit which counteracts, or tends to counteract, conspicuousness. In the majority of cases the bird's plumage is elusive, especially when the creature is at rest. A bird is very often just like a sample of the surrounding scenery of moor or meadow, hedgerow or wood. It is difficult to exaggerate the perfection of the garment of invisibility which protects a brooding woodcock or curlew among the withered debris of the wood or the bracken and heather of the moor. Protective coloration is not the exception, but the rule.

CHAPTER VIII

MIGRATION

§ 1. Main Facts regarding Migration. § 2. Problems in Process of Solution. § 3. Nature of the Migratory Custom. § 4. Immediate Stimuli liberating the Migratory Impulse. § 5. The Problem of Way-Finding. § 6. Possible Origin of the Migratory Custom.

MIGRATION is a seasonal mass-movement of a large contingent of a species from the breeding place, always in the colder part of the range, to the winter-quarters, and back again. It is not to be confused with the overflow movements of an over-crowded population, as in locusts and lemmings, or with a restless following of a mobile food-supply and the variations of physical conditions, as in the case of herring. From a slightly different point of view we may regard migration as an adaptive reaction to the difficulties presented by the seasons in particular areas. Just as some mammals circumvent the winter by passing into the state of hibernation to which they have become constitutionally adapted and predisposed, so many birds evade the winter by migration, and that not in virtue of individual initiative, but because of constitutional rhythms and impulses.

§ 1. MAIN FACTS REGARDING MIGRATION

(A) In the Northern Hemisphere the occurrence of migration is very general. But the extent of the phenomenon varies greatly. A flock of curlews may migrate from the moorland to the shore ; the Virginian Plover may migrate from Labrador to Brazil. In October, 1882, a vast multitude of Gold Crests struck our shores from the Channel Islands

to the Shetlands ; in most years the autumn tide from the Continent sets in much less noticeably.

(B) In a North Temperate country like Britain the birds may be grouped, from the migration point of view, in five sets :—

(1) There are the Summer Visitors, *e.g.* swallow, swift, cuckoo, nightingale, mostly insectivorous, which arrive from the south in spring, nest and breed within our bounds, and return southwards and south-eastwards in late summer or autumn.

(2) There are Winter Visitors, *e.g.* fieldfare, redwing, snow bunting, many northern ducks and divers, that come southwards and south-westwards to our shores in winter, and return northwards in spring to their breeding-quarters.

(3) In a set by themselves may be ranked the birds-of-passage in the narrow sense, *e.g.* the great snipe, the little stint, and some of the sandpipers, which rest on our shores, for a short time only, on their way farther south or farther north.

(4) There are many “partial migrants,” *e.g.* lapwing and goldfinch, which are always represented in the country in question, but not always by the same individuals. Some leave the country, others do not. Those of a particular locality move southwards in autumn, and their place is taken by a wave from farther north.

(5) There remain the strictly resident birds, such as in Britain the red grouse, the house sparrow, the rook, and the robin.

Perhaps another division should be made for “casual vagrants” or stragglers which occasionally appear far off their normal range, *e.g.* the American Kildeer plover in Aberdeenshire in 1867 or the Glossy Ibis in the same region in 1920.

(C) Birds breed in the colder area of their migratory range. Part of the reason is, no doubt, that the brooding birds and the nestlings are apt to suffer from the heat of the sun. Thus the general movement in autumn is southwards, or south-eastwards, or first westwards and then

southwards. The spring movement is on the whole northwards, with curves to the east and west. Besides the difference in direction, there seem to be differences in mood, for the autumnal flight is more dallying and the spring flight more impetuous. Audubon notes that the American rice-bird flies in spring by night and in autumn by day. In some cases the spring route is shorter than the autumn route, as if the birds drew the S—N.E hypotenuse of a triangle whose perpendicular was N—S and base W—E. In many cases the first representatives of a species to arrive in a North Temperate country in spring are the mature males; then follow the mature females; the immature birds bring up the rear. In the autumn the order tends to be reversed, the young birds leaving first. In the case of the aberrant cuckoo the adults leave Britain a month or more before the young birds, but this is an exception that proves the rule. The normal delay of the mature birds in autumn may be associated with the labours of nest-making and feeding the young and by the incidence of a late summer moult.

(D) In spite of minor perturbations, often due to the weather, there is no doubt as to general regularity of the migration movements. In different parts of a country the dates of the arrival and the departure of migrants vary within comparatively narrow limits. Like the dates of the appearance of wild flowers, they are determined by old-established internal rhythms correlated with external periodicities, though they may be swayed to one side or the other by the temperature and other physical conditions of a particular place or a particular year. Fog and headwinds may delay arrival, abundance of insects and mild weather may delay departure, but on the whole there is notable regularity in the comings and goings. It seems that the weather conditions that obtain when a migratory movement starts are of much more importance than those into which the birds pass in the course of their flight, for birds are not easily baulked when they get fully agoing.

Another side to the regularity is seen in the return of

the same bird to the same breeding place in successive years. A swallow marked in Aberdeenshire in 1912 returned to the same farmstead the following year. A swift "ringed" in Ayrshire in 1914 was recaptured in the same place in 1918, having doubtless been to Africa four times in the interval. The same regularity of return to the original homestead has been proved in the case of some other birds, such as the stork.

§ 2. PROBLEMS IN PROCESS OF SOLUTION

(a) **Routes.**—More facts must be collected before much can be safely said in regard to the migratory routes. The most useful data are those furnished by observers at lighthouses, lightships, and strategic inland stations, and by the "ringing" method. In "ringing" birds a very light aluminium ring of appropriate size, bearing a stamped number and address, is fastened to the instep region of the foot. A small percentage of these birds are afterwards heard of from distant parts, and if the rings are returned to the marking station with information as to the date and place of the bird's recapture, there is gradually built up a knowledge of the paths that are followed in migration. Thus rings put on storks in North Germany have been returned from Damascus, Alexandria, the Blue Nile, Rhodesia, the Kalahari desert, Basutoland, and elsewhere, so that Dr. Thienemann was able to conclude definitely that there is an autumnal migration of storks from the shores of the Baltic to South Africa.

"In the same way it has been made clear that there is among hooded crows, for instance, a great westward movement in autumn, *e.g.* from Finland along the shores of the Baltic, and that there is a subsequent curve towards the south. This westward and then southward curve seems to be true of many birds in North Europe. Certain contingents seem to swerve southwards by the valleys of the Rhine and the Rhone, and then across the Mediterranean to North Africa. Other contingents seem to go further westwards,

crossing, it may be, by way of Helgoland to the South of England, and thence across to France, Spain, and Portugal, finally landing like the others in North Africa. For some other birds, like the swallow and the Red-Spotted Blue-throat, there is considerable evidence of a more direct north to south movement in autumn. Large numbers of swallows are seen in autumn making their way down the west coast of Africa, perhaps reaching the Cape; those from Eastern Europe are said to work their way southwards by the Nile Valley. Corresponding species or varieties of swallow in North America seem to fly southwards to Brazil, and in North Asia to Burma" (Thomson, "The Wonder of Life," 1914, p. 172).

For European birds, Lucanus distinguishes three routes that have been satisfactorily demonstrated. *First*, there is the west coast route, which extends from east to west along the southern shores of the Baltic, along the coasts of France (and the southern coast of England), southwards to Spain, and across to Africa. Among the birds following this path may be mentioned—gulls, terns, snipe, oyster-catchers, lapwings, hooded crows, starlings.

Second, there is an Adriatic-Tunisian route. Birds gather in eastern and central Europe, and follow both coasts of the Adriatic to the southern end of Italy, whence they cross, *via* Sicily, to Tunis. This path is followed by some snipe-like birds and by many songsters.

Third, there is the Italian-Spanish route. Birds gathering in Hungary, Austria, and Southern Germany pass to the south of the Alps across the north of Italy, *e.g.* along the basin of the Po. Thence some may follow the coast of France and Spain to Gibraltar, while others cross by Corsica and Sardinia, or *via* the Balearic Islands. This route is followed by thrushes, starlings, plover, and many other birds.

(b) **Height in the Air.**—Another question requiring further investigation is as to the height at which birds fly in their migration. Some birds, *e.g.* larks, starlings, and thrushes, have been seen flying low in enormous clouds

across the sea, but this is not the way with the majority. Data have been arrived at in various ways. (1) By means of captive balloons Lucanus determined the height at which stuffed specimens of well-known birds became invisible. Thus a rook was a visible spot at 750–800 metres, but invisible at 1000. A buzzard was just visible at 1000 metres, which showed that Gätke's estimate of observing one at 3300 metres was quite out of the question. (2) Ornithological astronomers have sometimes identified migrants crossing the telescope's field and have estimated the height at which they were flying. Spill's estimates (quoted by Hilzheimer) gave 2000–3000 metres for many birds, but there is almost certainly some fallacy here. (3) In direct aeronautical observations Lucanus saw no migrants above a height of 1000 metres, which is, he says, the height that yields the optimum breadth of view.

In his recently published book on migration, Lucanus (1921) shows that there has been much exaggeration of the altitude of migratory flight. Apart from birds of prey, the maximum height scientifically observed has been 2200 metres—a unique case of small swallow-like birds; there are only a few records over 1000 metres; there are comparatively few between 400 and 1000. The great majority of migrants journey at an altitude below 400 metres.

High-flying birds like geese, cranes, and storks cannot be credited with an altitude of more than 1000 metres, though there is one case of what was probably a flock of cranes at 1400 metres. Of records above 400 metres there may be mentioned—a swallow at 450, a flock of cranes at 500, two storks and a buzzard at 900, and a lark at 1900 metres. An eagle tops the list at 3000 metres, but this was not in migratory flight.

(c) **Velocity of Flight.**—It is difficult to obtain secure data as to the rate of migratory flight, and many exaggerated statements are current. A carrier-pigeon has been known to fly at the rate of 55 miles an hour for four hours on end, and Gätke said that curlews, godwits, and plovers flew to oyster-beds four miles off in one minute. On very

insecure assumptions it has been calculated that Hooded Crows crossed the North Sea at a rate over 100 miles an hour ; that the Arctic Blue-Throat, leaving Africa in the evening reaches Helgoland next morning, having flown 1600 miles in nine hours, *i.e.* at a rate of over 170 miles an hour ; and that the Virginian Plover covers 3200 miles in fifteen hours, *i.e.* at a rate of over 200 miles an hour. This is preposterous.

A critical discussion by Lucanus (1921) disposes of such exaggerations. A stork does a good day's work when it covers 125 miles, though it may sometimes fly twice as far. It does not usually fly for more than six hours in a day. A quickly flying snipe, with the wind in its favour may cover 400-500 kilometres in 5-6 hours, *i.e.* at the rate of about 50 miles an hour.

A few figures of average migration-rate may be cited :—

Crane	30 miles an hour
Carrion Crow	30 " "
Finches	30 " "
Rook	32 " "
Crossbill	36 " "
Jackdaw.. .. .	38 " "
Starling	46 " "

The averages were established on the observed time taken to fly a measured distance (about a third of a mile) with the wind favourable and unfavourable. With a following wind the speed is increased by a considerable fraction, with a head wind decreased ; but there are limits, of course, to this. When the wind attains a high velocity, migration comes to an end.

(d) **Order of Coming and Going.**—The general proposition is probably true that the first arrivals in spring in a North Temperate country are the mature males ; they are followed a little later by the mature females, who sometimes find a nesting-place chosen for them ; the immature birds arrive last. More precise data are required before

we can say how many migratory birds conform to this rule, and how much elasticity there is in their observance.

The same remark applies to the autumnal flight southwards. The order is in general reversed, for the young birds are the first to leave and the older birds follow later. It is impossible to tell whether the flocks of young birds who seem to set off alone towards an unknown goal are or are not accompanied by a few old experienced hands who have made the journey several times before. We have mentioned the exceptional case of the cuckoo, where the callous parent birds leave Britain some six weeks or so before the young birds, who are left in the care of the foster-parents. Some of these foster-parents are non-migratory, so that these at least will not be in a position to help the young cuckoos on their southern journey.

(e) **Contrast of Spring and Autumn Flight.**—In addition to the differences in the order of their coming and going, there seems often to be a contrast in the manner of flying. In many cases the departure in autumn is gradual and hesitating—as if there was no particular hurry. The birds make false starts; they fly for some distance and settle down to feed again; they bid us a lingering farewell. In spring, when the impulse in the mature birds is partly sexual, there is more impetuosity. The flight is said to be in some cases continuous—the dotterel which sups in North Africa is said to breakfast next morning on the Scandinavian Tundra. The spring flight is said to be swifter than the autumnal flight and often shorter. It will be borne in mind, however, that all these statements come under the general heading “Problems in Process of Solution.” In regard to each and all it is necessary to have more facts.

§ 3. NATURE OF THE MIGRATORY CUSTOM

It seems useful to keep the word “habit” for routine established in the individual lifetime, but migrating is a racial custom, rooted in the hereditary make-up or organisation. It is the expression of a constitutional impulse, an

enregistered memory. What brings it into operation is an instinctive impulse, associated with internal rhythms of constitution and external periodicities in the environment.

Evidence that the migratory custom is of the nature indicated may be found in the occurrence of analogous phenomena in many organisms at very different levels of mentality—*e.g.* in land-crabs, in cels (where there is no return journey after reproduction), in salmon, in turtles, in seals. The relative measure of success that attends the adventure of migration, even when it is exhibited by the entirely inexperienced, points to the kind of behaviour we call instinctive. The impulse is inborn and the capacity of effectively obeying it is a ready-made power. Restlessness at the appropriate time is exhibited by *caged* birds (not cage-birds, like canaries) which have been made as comfortable as the misguided kindness of man can devise. It is not suggested that birds may not call intelligence to the assistance of their instinct, or that the power of successfully migrating may not be improved in the individual lifetime, but the trend of the evidence is towards the view that the impulse to migrate is instinctive and that the capacity of considerable efficiency in obeying this instinct is also part of the racial inheritance. In any case we must not think of North Temperate migrants flying south at the end of summer because of any definite prevision of the winter. They know no winter in their year, as the poet accurately observes, and have never known any, unless in the case of partial and incipient migrants. It is not by taking thought that these

“ wild birds change their season in the night
And wail their way from cloud to cloud
Down the long wind.”

§ 4. IMMEDIATE STIMULI LIBERATING THE MIGRATORY IMPULSE

A piece of instinctive behaviour is conditioned on its physiological side by a concatenated series of neuro-muscular pre-arrangements, comparable to those in simple reflex

actions. When a crumb of bread threatens to go down the windpipe instead of the gullet there is an involuntary cough, which is due to pre-arrangements between certain nerve-cells—sensory, intermediate, and motor—and certain muscle-cells. These pre-arrangements are part of the hereditary organisation. So it is with instinctive behaviour, but there is a chain of reflex arcs, and a succession of stimuli may be required. Moreover, many naturalists find good reason for believing that a piece of instinctive behaviour is often suffused with awareness and backed by endeavour. There is unanimity, however, in the conclusion that the neuro-muscular pre-arrangements, which form part of the hereditary structure, require liberating stimuli to set them at work. These stimuli may be from within or from without or from both. Our question concerns the liberating stimuli that lead to migration.

When eels that have been feeding and growing in a pond for a number of years reach a certain degree of reproductive maturity, a change takes place in their blood, thus there is more carbon-dioxide in it than is usual. The creatures become restless and they make their way from pond to river, from river to sea. An internal constitutional change serves as the liberating stimulus which sets the eels on their journey, and there are external stimuli, notably of temperature and pressure, which keep them going until they find the spawning area. Similarly, though we know almost nothing about it, the changes involved in the reproductive maturity of birds in spring pull the trigger of the impulse which leads them to leave their winter-quarters and make for their northern breeding places. This will not apply in the same degree to the immature birds, which also migrate. But there are external or environmental stimuli which also operate as trigger-pullers, notably the heat, the glare, and the drought. We must avoid the error of thinking that the liberating stimuli are causes in the sense that the impact of the cue is the cause of the movement of the billiard ball, they are causes in the sense that the releasing of the spring of a gramophone is the cause of

the music. We must avoid the other error of thinking that the stimuli act on the intelligence of the individual; they set into operation a predisposition enregistered in the race.

Of the constitutional change that follows the end of the reproductive period for the year we know almost nothing. The reproductive organs often dwindle into insignificance. A moult frequently occurs at this time. The growing scarcity of food, especially of insects, slugs, fruits and seeds, will imply hunger and its discomfort. The shortening of the daylight also leaves less time in which to secure the minimum rations. The increasing cold and the onset of stormy weather may also serve to awaken constitutional memories.

In some cases migration is a social affair, and it is likely enough that migrants of the same kin excite one another. Some young Black-Headed Gulls which we hatched and reared in the laboratory and afterwards set free in a garden, became interested at the time of migration in their kindred who flew overhead, and they eventually joined them. Matthew Arnold gives a beautiful suggestion of the social stimulus :—

“ And as a stork which idle boys have trapped,
And tied him in a yard, at autumn sees
Flocks of his kind pass flying o'er his head
To warmer lands and coasts that keep the sun,
He strains to join their flight and from his shed
Follows them with a long complaining cry.”

§ 5. THE PROBLEM OF WAY-FINDING

There is often great mortality during migration, and probably a discriminate elimination of those that wander. Some lose their way on the pathless sea and perish of hunger, others stray into areas which are too cold for them, others are fatally attracted to the lighthouses and dash themselves against the windows. Yet it must be admitted that the migration is often very successful: the birds find their way to their winter-quarters and they find their way back again. Can any light be thrown on their way-finding?

(a) It has been suggested that birds take advantage of all sorts of landmarks—mountain-ranges, river-valleys, coast-lines, chains of island. As birds have very acute vision, it would be hasty to rule out this suggestion, but it cannot be more than part of the solution. For many birds migrate during the night and many cross great tracts of sea which afford no landmarks. It is possible that there may be some sensory acuteness apart from vision, but the experiments that have been made have failed to detect this, and have made it improbable that the nostrils or ear-openings are of any importance in this connection.

(b) It has seemed to some naturalists that the success attending migration must be due to the cumulative inheritance of the results of experience. This is the attractive Lamarckian view, but it meets several serious difficulties. It is uncertain that the results of individual experience can be entailed on the offspring, and it is not evident what the content of experience could be in birds flying by night, at great heights, and over the trackless sea. In regard to the second of these difficulties it is open to the Lamarckian to say that the flying by night and at great heights and over the trackless sea is the final outcome of ages of evolution, and that one must think back to much humbler beginnings when the migrants flew by day and low and from island to island. Then, obviously, the experience would have a definite content. There remains the difficulty of the transition from the humble beginnings to the astounding outcome, the difficulty of finding evidence to warrant a belief in the cumulative results of individually acquired experience.

(c) A third suggestion lays emphasis on the social character of many migrations and suggests that a tradition may be kept up. Thus those who followed well for several years may become the leaders in the course of time. It would be unwarranted to say that tradition does not count in migration, but it cannot be more than a subsidiary factor. For it sheds little light on the original attainment of efficiency and it does not fit in well with the

belief that the young birds often migrate alone. At the end of the northern summer the young birds seem often to leave before their elders, and the exceptional case of the cuckoo, where the birds of the year migrate last, is not easier to explain.

(d) There remains the theory that birds have in a high degree what many animals show in a less degree—a sense of direction, the physiological basis remaining unknown. It is well-known that homing-pigeons are able to return to their cots from great distances, and this has been utilised by man for two thousand years. It can be improved in the individual by training, but the natural gift remains rather mysterious. A capacity for finding the way home is also exhibited by cats and dogs, horses and cattle, but the data are as yet too anecdotal to be of much value for scientific purposes.

Careful and prolonged experiments with ants and bees, which find their way home from a limited distance, favour the conclusion that the individual animals learn their area. They build up a knowledge of their environment, enregistering the significance of various sets of stimuli—olfactory, tactile, visual, and kinæsthetic (memory of movements taken). It must be admitted, however, that while we may go far with this theory of enregistering sensory stimuli so as to find “landmarks” in scents, surface, illumination, and so on, and of the ant’s remembering the turns and twists of its jungle-path, and of the bee’s remembering the general direction of its flight from the hive towards which in returning it makes its “bee-line,” there are residual phenomena as difficult to account for as the homing of pigeons.

Professor J. B. Watson and Dr. K. S. Lashley have made important experiments with the Noddy Terns and the Sooty Terns which breed in tens of thousands upon Bird Key, one of the Tortugas group. It marks the northern limit of the migration of these two tropical terns, so that if the birds are taken anywhere to the north they will find themselves in all probability in a region which they never

before visited. It was found that marked birds could return to their nests after being transported in closed baskets to Galveston in Texas, more than 800 miles away. Some returned in about six days, some took nearly twelve, some did not return at all.

Two Noddies and two Sooties were taken in the state-room of a steamer to Havana ; they returned next day to Bird Key, a distance of 108 miles. Of five birds liberated off Cape Hatteras at least three returned in a few days, having accomplished a journey of 850 miles as the crow flies, and of much more if the alongshore route was followed. Four Noddies and four Sooties were taken in a hooded cage on a Galveston steamer to about 461 statute miles from Bird Key and liberated where no shore line was visible. "On release all birds with one exception started east (homewards). That one headed west and continued for about 200 yards, then turned suddenly and started east." They had a strong head wind against them throughout the first day, but two of the Noddies returned in safety to Bird Key.

Dr. Lashley has shown that for short distances on the island itself the terns adjust themselves to the nest, their mate, and their young, on a basis largely of visual experience, helped a little by memory of movements, and sometimes by sounds. But the investigators are not prepared to offer any solution of the problem of distant orientation. They have proved that untrained birds can return successfully across the apparently trackless sea from a distance of 800 to 1000 miles, but they do not know how it is done. The possibility of utilising landmarks seems quite excluded ; there is no evidence that the retina of the bird is specially sensitive to infra-luminous rays ; there is no evidence that birds nose their way through the air feeling the direction, strength, and temperature of the wind as it plays on the mucous membrane of the nasal cavity. It is possible that there may be on other parts of the body tactile or thermal nerve-endings which react to slight differences in pressure, temperature, and humidity. There may be some sensitiveness

to magnetic waves. At least nine hypotheses have been suggested, but a basis of fact has still to be found.

Professor Watson makes an interesting observation on the duration of the nesting impulse when the normal procedure is interrupted by experiments such as he made. He finds that it remains strong for two or three weeks, and this gives an illumining significance to the homing. As we have said in our "Secrets of Animal Life," "the sea-swallows are returning to their nests, that is, to activities in which their life reaches its climax, to the continuance of which they are impelled by a deep organic urge, by an irresistible impulse which is not balked by any waste of seas."

§ 6. POSSIBLE ORIGIN OF THE MIGRATORY CUSTOM

(a) The Robber-Crab (*Birgus latro*) of the Pacific Islands has become thoroughly terrestrial, even to the extent of climbing trees, but it has to migrate to the shore to spawn, and its larvæ swim for a time in the open sea. It is a general biological rule that a new generation is started in the ancestral haunt of the race. The migration of the land crab from the hills to the shore is bound up primarily with its previous colonisation of the dry land, and secondarily with the fact that without great changes in the life-history the spawning must take place in the sea.

Several turtles have become pelagic animals, but they have to come to a sandy shore to lay their eggs. When these hatch and the young are able to fend for themselves there is a return to the open sea. Similarly, some at least of the sea-snakes, which live far from land, migrate to the shore to give birth to their young, and protect these for some time among the rocks. Seals, again, which have considerable emancipation from the solid earth, come to the shores at the breeding season. That this is not a necessary interruption of the aquatic life of a mammal that has ceased to be terrestrial is shown by the whales and dolphins.

It is clear that the migratory custom has in many cases

to do with finding a suitable place for breeding and for bringing up the young.

(b) In the life of many an animal the great difficulty of the year is the winter, and many of the ways in which this difficulty is met or evaded are familiar. Thus there may be a winter-coma or a true hibernation (in mammals); there may be a gathering of external stores; there may be an accumulation of internal reserves; there may be a protective change of colour; but, in a way, the neatest solution of all is migration. We may suppose, therefore, that migration of birds arose in regions where a change of climate made it difficult to face the winter. And even without postulating much change of climate we may see in the "partial migrations" which seem to be in process of evolution in some cases, *e.g.* lapwings, to-day, the advantage of seeking out optimum conditions—a cool place with plenty of insects and water for the breeding period, and a genial place, also with plenty of food, for the winter's rest.

(c) But there is a third factor to be recognised, the advantage of dispersal from an area that tends to become over-crowded after the breeding.

Given a certain initiative, which animals rarely lack, due either to the spur of necessity or the self-assertiveness of an adventurous spirit, we can understand how birds began the migrating device. It is one of the many answers-back which they have given in the course of their struggle for existence, and we have seen that its evolution would be justified by at least three advantages.

CHAPTER IX

COURTSHIP AND SEX

1. Physiological and Psychological. § 2. Modes of Courtship summarised. § 3. The Mating Behaviour of Pigeons. § 4. The Courtship of the Great Crested Grebe. § 5. The Observations of Selous. § 6. The Evolution of the Voice. § 7. The Variety of Bird Song. § 8. The Vocal Organs. § 9. The Interpretation of Song. § 10. Reconsideration of Darwin's Theory of Sexual Selection. § 11. Sex-Characters. § 12. Hormones and Sex-Characters. § 13. What determines Sex ?

§ 1. PHYSIOLOGICAL AND PSYCHOLOGICAL

THE first chapter in the Reproductive Cycle is courtship. This implies biologically a heightening of the sex-impulses which makes the consummation more certain and more successful ; but it may also have a psychological significance in binding the mates together, in establishing psychical links, as may be illustrated by the case of the Great Crested Grebe. It is difficult to steer a middle course between crediting the pairing birds with too much associated feeling and allowing them too little, especially difficult because the courtship behaviour of birds has been carefully studied only in a few cases. It should be noted that the courting does not always lead up to sexual union as its immediate climax, and that there is sometimes a sort of " engagement " period. It should also be noted that a snatch sexual union may occur apart from any courtship ceremonial and apart from subsequent co-operation of the parties. To get a fair estimate for the present time it may be useful to discuss two cases that have been very carefully studied, the case of pigeons, studied by Whitman (1919), where the physiological aspect is the more dominant, and the case of the Great Crested Grebe, studied by Julian Huxley (1914), where the psychological aspect is more definitely expressed.

§ 2. MODES OF COURTSHIP SUMMARISED

- A. Appeals to Sense of Hearing :—
 Song, twittering, cooing, crowing, calling, flapping of wings.
- B. Appeals to Sense of Sight :—
 Display of plumage and of skin-ornaments such as wattles.
 Display of movements showing agility and grace, in strutting, parading, fluttering, flying.
 Often repeated rhythmical movements, *e.g.* bowing, curtsying, dancing; “ suggestive ” movements, as when the male jumps over the female (pigeons).
- C. Appeals to sense of touch :—
E.g. when male chough strokes the head of the female with his bill, when male pigeon presses his neck over that of his desired mate, when male pigeon receives in his open mouth the bill of the female.
- D. Chasing the female on the ground or in the air, or driving her towards the nest.
- E. Varied subtler modes, some of which may have a symbolic significance, *e.g.* when the Great Crested Grebes offer water-weed to one another.

§ 3. THE MATING BEHAVIOUR OF PIGEONS

The prolonged observations made by the late Professor C. O. Whitman (1919) on various kinds of domestic pigeon and wild dove yielded many very interesting results.

The impulse to sexual activity is primarily from within, arising for the most part automatically, but the fire is fanned by the mutual influence of the sexes, and it may be intensified or depressed by extrinsic influences such as diet and weather.

The impulses arise synchronously in the two sexes, but it is normal for the male to take the initiative in beginning the cycle. Modifications of the usual behaviour will result if the two birds are very different in their state of readiness ;

thus the sex-impulses, which are usually satisfied for the time being in about a week, after which comes the period of egg-laying and incubation, may be prolonged. It is also noteworthy that a female domestic pigeon may pass to nest-building, egg-laying, and incubation without the stimulus of a mate, but the unfertilised eggs come, of course, to nothing.

While it is normal for the male to take the initiative, the rule is often broken. In connection with this and with the futile mating of two females, it must be noted that "sex-intergrades" often occur among pigeons. Professor O. Riddle (1914) has made a study of extremely masculine females. These relatively abnormal forms point the way to cases like the Phalaropes, where the female birds normally take the initiative in courtship and the males do most of the incubation.

The preliminary acts which Professor Whitman studied in male pigeons are thus summarised by the editor, Dr. Harvey A. Carr (1919, p. 93): "billing or pecking at their own feathers on the wings and certain parts of the tail; preening and shaking the feathers; elaborate bowing and cooing; going to the nest and giving the nest-call; approaching the mate; giving amorous glances; wagging the wings; lowering the head; swelling the neck; raising the wings; raising and spreading the tail and feathers on the back and rump; alternately stamping and striking the feet and wagging the body from side to side, and strutting with drooping wings. Charging and driving may be resorted to in the courtship. The male walks or rushes at the female, holds the head high, lowers the wings, exhibits excitement, elevates the back, erects the feathers, pecks perfunctorily or petulantly, clucks, and gives the driving coo consisting [in bronze-wing pigeons] of three notes, with raised wings, raised and spread tail, while the beak is on the floor."

This summary is too much like a composite photograph: it blurs the fact that the behaviour is often in a marked degree specific for particular kinds. Thus male mourning-doves (*Zenaidura*) and some others stamp with their feet before their desired mates; the male bronze-wing stands on tip-toe,

lifting first one and then the other foot, raising one side of the body and then the other "in a way to exhibit his iridescence in different lights." What Darwin described in a red tumbler, "walking with its wings raised and arched in an elegant manner," is very common, and along with specificity of behaviour we must also note that genera very different from one another may share the same peculiar habits.

It is of interest to note that particular kinds of behaviour marked in courtship may also be exhibited when the bird is emotionally excited in other connections. Thus Whitman notes that the raising of the tail to 45° or more is exhibited by the male *Geopelia humeralis* when he is trying to drive away another cock as well as when he is displaying before his desired mate.

The rhythmic repetition of movements—seen in bobbing and curtsying, swaying the body from side to side, lifting the feet alternately—may have, especially when accompanied by cooing, a suggestive effect on the female, just as opening the gape wide suggests to the female that she should put her mouth in.

That the male seeks to arouse first the interest and then the excitement of the female is certain; that other males are aware of the sexual significance of the preliminaries is also certain; the error to be avoided is supposing that the male is directing his behaviour in detail towards the satisfaction of the sexual impulse. The behaviour exhibited in the courtship ceremonial is instinctive, specific for the race, and the outcome, doubtless, of a long process of selection in which ineffective displays were eliminated.

In some cases, such as the bronze-wing, the male drives and charges the female, and there is no doubt that this means "Go to the nest." The driving is often accompanied by the utterance of the "nest-call," which is characteristic also of the incubation-period. The question rises whether the nest is not primarily the stage on which sexual union is consummated, a theory that would make the driving and charging more intelligible.

To return to the editorial summary of Professor Whitman's observations. "As the period of consummation approaches, the composition of the activities changes with the addition of new elements. Along with bowing, there is billing and fondling of each other's head, hugging or necking, jumping over the female without any attempt at mounting, opening the beak by the male, inserting of the female's beak in his, and often the shaking and rattling of the crop as if the male fed the female. The female stoops with lowered head, the male mounts with a jump, the female raises her wings as a support and lifts the tail, while the male reaches back, moving the tail from side to side until contact is effected."

Some features in the later courtship behaviour are suggestive of, or tend to induce the attitude of sexual union. This may be said of the way in which the erotic male jumps quickly over the back of the female, or of the way in which the birds hug one another by the neck. In many different kinds of pigeons the male receives the female's mouth within his own, and he may regurgitate a little food. This close contact of surfaces may increase the sexual excitement as in amatory kissing, but it is possibly suggestive, since both parents feed their young in a closely similar fashion. "In many organisms there seems to be an intimate functional relation between the sexual activities and those processes involved in the care and feeding of the young" (Whitman, 1919, III. p. 107). Dr. Riddle observed that two old males which incubated eggs and fed the young, prolonged the feeding period till eventually the sexual note was struck on both sides. The young bird was at first primarily interested in the *food*, but the continuance of the activity finally aroused a sexual response before maturity (*ibid.* p. 108).

§ 4. THE COURTSHIP OF THE GREAT CRESTED GREBE

The sexes in grebes are quite like one another, the usual plumage being dusky brown or blackish grey above and silvery white below. The glossy satin-white of the lower

plumage leads to considerable mortality at man's hands, but one is glad to know that the birds are not easily shot. Some kinds have in both sexes special decorations put on at the breeding season, such as crests and tippets of a golden chestnut colour. In this respect, Professor Newton remarks, the Eared Grebe (*Podiceps auritus*) is particularly remarkable, "the head being surrounded, as it were, by a nimbus or aureole, reflecting the rays of light, and glittering with a glory that passes description." But it is the courtship behaviour that is most striking, as Mr. Julian Huxley showed some years ago in his careful study of the Great Crested Grebe (*Podiceps cristatus*). (1) "Under the force of rising



FIG. 36.—Courtship of Great Crested Grebe. (After Julian S. Huxley.) The female in the so-called "cat attitude" of display. This is also exhibited by the male.

emotional tension" a bird waggles its head, first gently and then violently; the possible mate follows suit; and a bout of shaking ensues, interrupted at short intervals by a slow side-to-side swinging and by curious backward bending of the head as if to preen the wings. After a dozen or fifteen violent shakes, with a corresponding number of slow swings and liftings of the wings ("habit-preening"), the two birds suddenly relapse into the normal. (2) A hen comes swimming across the water, calling for a mate, on whose appearance she suddenly assumes first a "Dundreary" and then a "cat" attitude, while he, appearing beside her after a long "ghost-dive," "grows" up out of the water, standing save for a few inches erect, like "the hypnotised phantom of a rather slender penguin." He sinks slowly down again;

she ceases to be like a fat cat ; they have a short bout of head-shaking ; and after a little they preen their feathers and go off to fish. (3) But there is still more complex behaviour. After prolonged head-shaking and wing-lifting, during which the crest came to look like " a large chestnut-and-black Elizabethan ruff," both birds dived, and when they reappeared each held in its beak a bunch of dark ribbon-like weed, pulled from the bottom. They came up at a distance from one another, but swam rapidly together. When about a yard apart they both rose up from the water into an erect position, in the " ghostly penguin " attitude, their brilliant white breasts touching. After rocking gently from side to side, their feet working hard all the time, they sank very gradually on to the surface of the water. The weed, whatever it means, disappeared during the " penguin dance," and, after a bout of rather excited shaking, the two birds drifted apart and began to pick food off the surface of the pond.

We see then that the courtship ceremonial consists of various combinations of head-shaking and habit-preneing, of love-calls and mutual discovery, of Dundreary and cat poses, of " ghost-dive," " weed-trick," and " penguin-dance " ; but what does it all mean ? To this question Mr. Julian Huxley gave an answer which strongly commends itself to us : that " the courtship ceremonies serve to keep the two birds of a pair together, and to keep them constant to each other." It will be plain from what we have cited that the self-exhausting ceremonial does not lead directly to pairing ; it must have a subtler significance than mere excitation. It is a means of establishing an emotional bond. " Birds have obviously got to a pitch where their psychological states play an important part in their lives. Thus, if a method is to be devised for keeping two birds together, provision will have to be made for an inter-play of consciousness or emotion between them." By means of the courtship ceremonial the two birds become better acquainted, an " emotional companionship " is established, and this helps to ensure the success of the subsequent co-operation in

PLATE V



COURTSHIP OF GREAT CRESTED GREBE (after Julian S. Huxley).

The two birds engaged in the so-called "penguin dance," rising high out of the water, breast to breast, often holding weed in their mouths.

which the cock and the hen play nearly equal parts in all activities concerned with the family. We are, in fact, face to face with an elaborate and slowly wrought out sex-ritual which raises physical attraction to the level of psychical affection, fondness to love, in short.

The courtship ceremonial varies from species to species. Thus in the American Western Grebe there is a remarkable "water glide" and also a "wedding dance," in which the two birds, with moss in their mouths, circle round three or four times, breast to breast, in an erect position in the water. In some species the voice counts for much; thus we read of Holboell's Grebe that "one of the birds would start with a long wail and then the other would chime in with a similar note, both winding up with a series of quavering cries very much like the repeated whinnies of a horse. During these vocal demonstrations the neck would be thrown forward and the head and bill tilted upward at an angle of 45° ." The love-song of the Horned Grebe consists of a series of croaking and chattering notes, followed by several prolonged piercing shrieks; in some other species there is an approach to mellowness.

Whether we take Mr. Pycraft's admirable study "The Courtship of Animals" (1913), or a particular case like that so thoroughly observed by Julian Huxley, we are led to the conclusion that courtship-habits often have great intricacy and subtlety, and that it is impossible to exclude the psychical factors. Let us quote Huxley's summing-up:—

"Display and ornament do not act on the æsthetic sense of the female, but on her emotional state; they are—using the words in no narrow or unpleasant sense—excitants, aphrodisiacs, serving to raise the female into that state of exaltation and emotion when alone she will be ready to pair. . . . But the element of choice does, in another form, remain. In animals such as birds, where there is a regular pairing-up season, and where, too, the mental processes are already of considerable complexity, it is impossible to doubt but that mating may be, and in some species

is, guided by impulse, unanalysable fancies, individual predilection."

§ 5. THE OBSERVATIONS OF SELOUS

Of great interest, and, as it seems to us, of great importance are the numerous observations recorded by Edmund Selous, which certainly corroborate Darwin's view that the female plays a real part in selection. We wish to give some characteristic illustrations chosen from the abundant first-hand data which this distinguished naturalist has collected.

In mallards there is apparently affectionate companionship not directly associated with sexual satisfaction. "Instead of separating, they continue to swim side by side in the most affectionate manner, and whichever of the two may take the initiative in going anywhere is closely followed by the other. This continues hour after hour, right through the morning, deep into the afternoon—for the whole day, there can be no doubt, were one to set it out, and so for day after day. Moreover, the intervals between the performance of the nuptial rite are considerable—several hours, it would seem. Envisaging these facts, and observing the whole manner of the two birds, to me it seems evident that friendship and affection, irrespective of sexual appetite, keep such pairs together. Their married relations are, in fact, very like our own, at their best, and if it be said that we cannot argue from ourselves to other animals, it is certainly less scientific to *assume* a difference in kind, in spite both of appearances and the known facts of evolution." Where Mr. Selous is perhaps mistaken is in the interpolation "irrespective of sexual appetite." The safer position is that alongside of the sexual appetite there are psychical linkages analogous to affection.

It may be that the dawning sense of property and preserves may find expression in the way one pair of oystercatchers will hunt another pair, all four piping, or a pair will unite to drive off a bold intruder (Selous, 1906). But

perhaps there is not much more than fun in many episodes of this sort.

“ Two redshanks, after pairing, run in an excited and curious-looking manner, over the sand, following one another ” (Selous, 1906). There is similar behaviour in avocets and peewits. Perhaps it is of the nature of a display ; perhaps it is a means of riveting bonds of comradeship.

In regard to the Redshank, the following description is given by Selous (1906) : “ The male, advancing to within some two feet of the female, continually waved and fluttered his wings above his back, holding them well aloft, whilst, all the while, uttering a little tremulous note, and nervously moving his red shanks. He did this for a considerable time—perhaps a minute—the effect, of course, being very striking ; and then, rising on the wing, fluttered, for a little, just over, and about a foot above, her, before dropping down for the actual performance of the rite.” As a matter of fact, as Mr. Selous points out, the male is rather *behind* than in front of the female, but “ his waved wings are, so to speak, all about him,” and “ with an eye on each side of her small head, the slightest turn of this—and it is always in motion—would enable her to see the whole person of the male.” There can be no doubt that she sometimes *seems* to be interested in the male’s display of his white tail, of the silvery grey under-surface of the wings, and of the coral-like legs, and that in other cases she is more indifferent although the display is equally effective. There can be little doubt that the male is seeking to excite her sex-interest in him.

Evidence of active interest on the female’s part is of importance. Selous (1906) describes the hen Kentish Plover’s participation in the combats of rival males : “ She was not satisfied with being a witness of the scene ; she took upon several occasions—perhaps a dozen—an active part in it. Running down to where the two were contending, she made little flies to one or another of them, but whether to both, or one only, or one more especially, I cannot say. The effect of these approaches, on the two males, was always to

make them more bellicose. . . . A third male was seen approaching, and, after a while, he entered into the area of the conflict, with a view, as it seemed, of joining in it." The hen bird flew at this intruder persistently and finally drove him off. It may be, as Selous says, that the female considers two rivals as the proper number. He suggests that this may have some bearing on the common sight, in spring-time, of three birds, and no more, flying together—three larks, three meadow-pipits, three peewits, three oyster-catchers, and so on. "Also, if we think of the female bird as able and ready, on occasion, to drive off any male, *vi et armis*, we shall the less easily regard her as the mere passive submitter to the male's superior force."

Mr. Selous (1906) points out that the male redshank's banner-like waving of his wings is certainly addressed to the female, that it occurs whether other males are about or not, and that it means a solicitation of the female's consent to go further. The female may move away or may fly at the male, frustrating his intentions. "This is a good illustration of the power of the hen bird in such matters, and how essential her co-operation is." The banner-like waving of the wings is a solicitation, for it is necessary to obtain the female's consent. "That he is addressing himself to the female, and to her only, and that she knows he is, is obvious, quite manifest, not to be doubted by any one who has seen the thing. It makes no difference whether other males are about or not; nor do males, when fighting or about to fight, act in this way." It is not a war-dance, but a wooing. The only difficulty is that the male is usually *behind* the female, not in front. But the female redshank, just like a woman, can see behind her.

In some birds like redshanks there is prolonged fighting between males, as well as displays before the females, and perhaps Mr. Selous is right in thinking of a double selection, "neither the handsomest nor the most vigorous *only* being chosen, but the handsomest among the most vigorous." It has not been found possible to follow an individual male combatant (among redshanks) from day to day, but the

contention of a pair is often prolonged ; and this suggests that neither of the rivals is able to coerce the female. A complexity is introduced by one of Mr. Selous' interesting observations on the Kentish Plover. Two males had been fighting for an hour or more, when a female appeared as an interested spectator. Another female approached and was driven off by the first hen, who also attacked a third male who appeared on the scene. But the second hen persisted for over an hour, until her jealous rival grappled with her desperately and drove her off. The mistress of the situation then proceeded to drive off one of the fighting cocks.

Courtship of Ruffs.—Mr. Selous has given a detailed account of the breeding habits of the Ruff (*Machetes pugnax*). The gathering place or *lek* is a flat strip of grassy shoreland, with tufts and rooted turfs here and there, and with worn circular depressions. The males appear in April and in great form. They race over the ground or at one another, with heads bent down and feathers out-ruffed. " They rush for some yards, then stop suddenly in a crouching attitude with the head extended forward on the ground, the legs bent, the feathers ruffed. In this position they remain for some time motionless, the body brought suddenly into a state of rigidity, which, however, is of the bent bow order, threatening each instant a renewal of energy. This may issue, shortly, in another furious run in a reversed direction, but often there is nothing further, and the bird, sinking more and more down till it lies along the ground, becomes gradually quiescent " (Selous, 1906, p. 292).

The fighting is carried on with great energy and zest, but no serious injuries are inflicted, and a minute after a serious encounter two ruffs are the best of friends. They are very sociable birds, and their jousting is no contradiction to their sociability.

There is no doubt as to the violence of the duels. Mr. Selous writes (1906, p. 422) : " The birds fought most furiously, kicking one another, hitting out with their wings, and seizing one another with their bills. They separated several times, one, when this happened, being generally

worsted for the moment, and pursued by the other, till, outdistancing him, he turned, and, crouching, rushed furiously on him again. This lasted, perhaps, some three or four minutes, and then ended by mutual consent, perhaps through mutual exhaustion, for the birds fought like demons—yet not harder, I think, than coots.”

When the females or reeves appear on the scene, the bustle of the tournament increases. The jousts last for a longer time and the excitement is great—among the ruffs. For “though the reeves often hurry out of the way of their turbulent admirers, yet they were quite cool and collected, seeming accustomed to the scenes they created, and to know what it all meant.” Mr. Selous satisfied himself that a reeve sometimes selects a male from amongst ten or a dozen, and is unmistakable in indicating preference and in making coy advances. The reeves seem to have great power in the assembly, and Mr. Selous is very emphatic in his conclusion that though the ruffs press about the reeve, they attempt no bullying. They behave “as if they are governed by the consciousness of being able to do nothing without the co-operation of the reeve—she must first signify her wish. Of display there is something, but it is not such a set or formal display as in the case, for instance, of the pheasant or the pigeon—excitement seems to hinder this. The best example of it is when a bird, darting, first, right away from her, turns, and darting back again, right to her side, with ruff swelled out, and wing (I think on her side) drooped, seems, for a moment, as though he would overwhelm her with his gallant show, but, the next, sinks prostrate at her side, and remains thus glued to the earth.”

“As for the reeve, everything about her, her every action—still more her inaction, her easiness and unconcern—suggests that she is complete mistress of the situation, that every ruff on the ground is absolutely dependent on her will. In fact, she seems the plain and unconcerned little mistress of a numerous and handsome seraglio, each member of which, however he flounce and bounce, can only wait to be chosen.”

At the height of the breeding season the scene on the

hill of Venus is lively. " Birds dart like lightning over the ground, turn, crouch, dart again, ruffle about each demure-looking, unperturbed little attraction, spring at each other, and then, as though earth were inadequate as a medium of emotional expression, rise into the air and dart around overhead, on the wing. The air resounds with the frequent dull shock of bodies, and the violent whirring of wings ; it is all motion, all energy, at the very fever-point of excitement, and then, all at once, a sudden cessation, almost a sudden death—only the feathers of each bird's back to be seen, or the tops of their head-gear, or ruff, or tail-feathers waving, here and there, in the wind, as they lie in tense, rigid immobility, like so many little bows of Ulysses, bent by themselves and ready, each moment, to spring back " (Selous, 1907, p. 163). And then, after an interval, there are preferences and pairings, the reeves caressing their chosen mates and soliciting them, so that a favourite ruff may pair more than twice as often as all his rivals together.

The important general inference that Mr. Selous drew from his observations is " that the reeve has the full power of choice, and that she exercises it in such a manner as to make it evident that she chooses this or that bird for himself, for something about him, that is to say, by virtue of which she likes him better than another, either always or at this or that time. I believe that this something is, in the main, his appearance, and that in so far as vigour may be a selected quality, it is selected only incidentally to this, which, however, would often be the case " (1907, p. 381).

In the case of the Blackcock Selous distinguishes between the formal display before the female and the totally different ecstatic leaping into the air, which does not seem to be significant in courtship. He believes that the so-called combats are of minor importance and not very serious ; the important activity is the display which prepossesses the female, and in this the cock exhibits all his best points. The female plays a quite indispensable part ; the display cannot go on without her ; she is jealous, even to assault and battery, of other females, during its continuance ; she gives evidence

of the influence of the display upon her ; she is won by it.

We have given prominence to Mr. Selous' observations because they seem to us to afford cumulative evidence of the reality of sexual selection in the narrower Darwinian sense—of preferential mating on the female's part and on the determination of preference by the male's success in arousing and focussing sex-interest.

Auks.—The courting guillemots twine their necks together, nibble at one another's plumage, bow profusely to one another, wag their heads from side to side, interlock their bills and sway their bodies. One is often seen running its bill down the front of the breast until it reaches the rock, then jerking it up again. This is like a male's performance ; but, as the sexes are practically identical, it is difficult to tell what part is the cock's initiative and what the hen's response. They seem to be monogamous, and both parents share in brooding (as their worn patches show) and in bringing food to the young bird. The same is true of the nearly related razorbills, but they are more vocal in their courtship, and while they resemble guillemots in their billing and nibbling caresses, they do not indulge in the profuse bowing ceremonial. We mention a detail like this because it illustrates the individuality or *specificity* of nearly related forms. In the case of puffins, which belong to the same auk family, there is a good deal of fighting among the males at the breeding season, and there is billing and bowing between the sexes. The head is often jerked upwards with the yellow mouth wide open.

§ 6. THE EVOLUTION OF THE VOICE

For many millions of years there was no sound of life upon the earth, and among Invertebrates there is no voice, nothing more than the instrumental music of chirping insects. This is produced by rapidly moving one hard part of the body against another. The first animals to have a voice were Amphibians ; that is to say, they have vocal cords which

produce a sound when the out-breathed air passes rapidly over them. Now there seems no doubt that the original use of a voice was as a signal between would-be mates, for that is its use to-day in the humblest vocal animals—the frogs.

But in the course of evolution the significance of the voice broadened out. It became a parental call ; it became an infant's cry. Thus the unhatched crocodile pipes from within the egg which is buried in the ground, and the mother hearing this cry unearths the eggs, and saves her offspring from being buried alive at birth.

Broadening still, the voice became a kin-signal, enabling members of the same species to recognise one another in the dark and in the intricacies of the forest.

Ages passed, and the voice rose on another turn of the evolutionary spiral, to be expressive of particular emotions outwith the immediate circle of sex—emotions of joy and of fear, of jealousy and of content. Later on, the animal began to give utterance to particular " words," indicative not merely of emotions, but of particular things with an emotional halo, such as " food," " enemy," " home." There can be no doubt that such birds as rooks have several words.

To man belongs the prerogative of using words as counters or symbols in his intellectual processes and of expressing judgments in sentences. What began as a sex-call became a medium of rational discourse.

§ 7. THE VARIETY OF BIRD SONG

Birds inherited their voice as part of their legacy from reptilian ancestors, among which it had probably become a kin-call, a means of telling certain pieces of news, and an expression of emotion. Birds re-invested this legacy, as it were, in their own avian constitution, and thence came song. It would be plainly a misunderstanding to think of the song of the mavis or the lark as having evolved directly from the croaking of frogs.

One does not forget that there are many birds that do

not sing, just as there are many birds that do not make a nest, but singing and nesting are characteristic of birds, and the simplicity or complexity of their expression is of minor moment. But what an extraordinary gamut there is in bird song. "It seems impossible," said Professor Newton, "to draw any but an arbitrary line between the deep booming of the emeu, the harsh cry of the guillemot (which, proceeding from a thousand throats, strikes the distant ear in a confused murmur like the roar of a tumultuous crowd), the plaintive cry of the lapwing, the melodious whistle of the widgeon, 'the cock's shrill clarion,' the cuckoo's 'wandering voice,' the scream of the eagle, the hoot of the owl, the solemn chime of the bellbird, the whip-cracking of the manakin, the chaffinch's joyous burst, or the hoarse croak of the raven."

To the scientific ear the ostrich's roar (which may be mistaken for a lion's) sounds like the coo-rooing of the dove. The shearwaters, which the greatest of our scholar-naturalists has identified with the birds into which Diomedes' companions were transformed, express in their cries, like the wailing of little children ("lachrymosis vocibus"), the same fundamental motif as the lark does, in its "lithesome, sibilant, and unceasing" song. Both in shearwater and lark, however, the vociferousness has passed beyond the confines of sex.

One of the strangest of cries is that of the Stone Curlew, "a weird discordant clamour, with something uncanny and blood-curdling about it, as though an inferno had suddenly been let loose on earth. We call them 'shriek owls' on this account, and it is not a bad name. Their wild cries ringing out loud and clear, then suddenly ceasing and intensifying the silence of the still summer night, are something suggestive of murder and sudden death."

Biologically regarded, the song of birds is marked by its specificity—a cold-blooded way of saying that it is expressive of a distinct individuality. Each bird-personality expresses itself in its own way. Thus according to John Burroughs: "The type of the lark's song is the grass, where the bird makes its home, abounding, multitudinous, the notes nearly all alike, and all in the same key, but rapid, swarming,

prodigal, showering down as thick and fast as drops of rain in a summer shower." Thus Brehm writes: "Dominated by love, the jay sings, whistles, and murmurs, the magpie chatters, the croaking raven transforms its rough sounds into gentle, soft notes, the usually silent grebe lets its voice be heard, the diver sings its wild yet tuneful ocean-song, the bittern dips its bill under water that the only cry at its command may become a deep, far-sounding booming."

What is the unity in all this diversity? It is that each bird is *primarily* saying, according to its mood and skill: "Hither, my love, here; here I am, here!" But the song of birds will be woefully misunderstood if we simply write it down as an elaborate sex-signalling. It is that primarily, just as serenading is, but it is much more. In true songsters at the pairing season the song is indicative of passion; it is a soliciting of the female's attention, interest, and acquiescence. But it has come to be an expression of emotions that have gathered round the passion of fondness, and it may manifest itself away from any immediacy of sex-desire. We have a peculiar right to insist on this in the case of birds because sex-activity is in most cases very sharply punctuated among them; there is a waning of the reproductive organs after the breeding season is over. But it is well known that many birds have a second singing after the tide of sex has ebbed for the year. It would be unwarrantable to say that song may pass entirely beyond the confines of sex, for that would mean a denial of the unity of the organism. But the facts indicate that it may pass far beyond being an expression of sex-desire.

§ 8. THE VOCAL ORGANS

Whereas in mammals the vocal cords are in the larynx, at the top of the windpipe, in birds they are situated in a special song-box, the syrinx, at the foot of the windpipe, where it branches into the two bronchial tubes leading to the lungs. Birds have a larynx, but it is voiceless—one of the

little differences proving that birds and mammals are on divergent evolutionary tracks.

The song-box or syrinx is a transformation of the lower end of the windpipe or trachea, usually helped by the uppermost rings of the bronchial tubes—an illustration of that familiar method of evolution which consists in making a new thing out of some structure actually very old. The bird's syrinx is a distinct novelty, and yet the materials for making it are present in the reptile.

The syrinx is anatomically intricate, but the essentials are: (1) the firm, bony framework, sometimes dilated into an accessory resonating sac, as in the diving ducks; (2) the vibrating internal membranes over which the out-breathed air passes rapidly, producing all the many sounds; (3) a variable number of muscles which alter the tension of the membranes, and may also move the windpipe as a whole; and (4) the controlling nerves, notably the two hypoglossals from the brain.

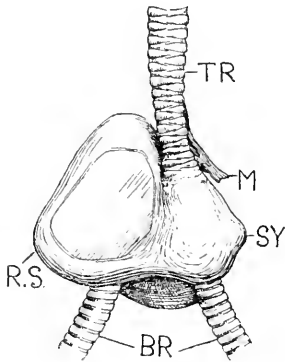


FIG. 37.—Song-box or syrinx of a diving duck. From a specimen. TR., trachea or windpipe; M., a muscle moving the trachea; SY., the syrinx or song-box containing the vocal cords; R.S., a special resonating sac; BR., the bronchial tubes leading to the lungs.

The song-box is usually more complicated in birds with a reiterated, modulated song with several phrases than in those with simple calls and pipings. But it is not possible to establish any exact correlation between the intricacy of the song and the complexity of the instrument. Thus crows have a very complicated song-box, but are not songsters,

though it may be said, of course, that the complexity is here associated with talkativeness and large vocabulary. The fact is that the musician has to be considered as well as the instrument, part of him though it is.

§ 9. THE INTERPRETATION OF SONG

There are two extremes in the interpretation of the song of birds. The first is too materialistic ; it leaves the mind of the bird out altogether. The second is too generous ; it allows too little for the body, too little, for instance, for the hormones which pass from the reproductive organs of the male and, being distributed through the body by the blood, prompt the full development and activity of certain parts, such as the syrinx. Similarly in the female there are hormones which inhibit the expression of masculine characteristics, such as song. In "crowing hens" and similar phenomena there is either atrophy of the ovary or some testicular development.

Amongst songsters the syrinx of the female often shows a grade of evolution—or should one say development?—distinctly lower than that of the exuberant male ; and this is, of course, associated with the fact that the female may have no song at all, or only a little. The probability is that hormones from the ovary inhibit the development of the female syrinx.

It has been proved, in a few cases, that a young bird artificially hatched can utter certain sounds characteristic of its kind. The peewit will say "Peewit," or something very like it, the moment it is hatched, and a cry from within the egg is sometimes heard. This points to the instinctive or hereditary nature of the ability to utter certain characteristic notes. There is a counterpart of this in the way in which some young birds, such as partridges, respond instantaneously to the parental alarm note when heard for the very first time, though they remain indifferent to the more urgent warning of their foster-mother hen.

But while a certain amount of vocal ability is part of the hereditary make-up, there seems little doubt that the gift requires educating. The song of the first year is sometimes inclined to be tentative and generalised. It improves with practice, and is probably helped by emulation and imitation.

The way in which some birds, *e.g.* skylarks, steal snatches of one another's music suggests the importance of imitation as a factor in educating the vocal powers.

Biologically regarded, the song is a partly instinctive, partly deliberate endeavour on the male's part to attract his desired mate's attention, to commend himself to her senses, to excite her sex-interest, and to overcome her coyness. There is a great deal to be said in support of Darwin's thesis, elsewhere discussed, that the singing powers of the male birds have been enhanced in the course of many generations because the better singers tended to be more successful in their love-making. But we must not think of a piece-meal evolution. On the one hand, the song is the expression of a unified organisation which includes strength of heart and lungs as well as of vocal cords. On the other hand, we must not think of the female bird listening with a critical ear, and rejecting a suitor who makes a false note. It is rather that she gives herself in the course of time to the male whose total impression on her decisively excites her interest and awakens her desire.

But what we wish to add to the ordinary biological interpretation is a recognition of the fact that birds are emotional personalities, that to the passion of physical fondness there has been added a joyous affection. We cannot prove this for the bird, nor for our fellow-citizen. In both cases, it looks as if it were so, and if our fellow-citizen denied it we should not believe him.

Emotion tends to be accompanied by motion. "And then," as Wordsworth said, "my heart with pleasure fills, and dances with the daffodils." In the courting bird the internal motions associated with singing are in line with the external movements of fluttering, leaping, dancing, and soaring. Singing is an expression of emotional excitement.

It is well known that when the young ones are hatched out in the nightingale's nest, the male bird's lyric is replaced by a solicitous parental croak, though he may recover his voice and sing again if love's labour be lost before his constitution changes for the year. But this simply implies that

in the natural course of things one set of emotions succeeds another, just as one set of motions and bodily functions succeeds another. These are the golden and silver faces of the bio-psychic shield. We mean that there is an emotional concomitant of the nightingale's anxious guttural croak after the brood is hatched, just as truly as there is in the early summer nights, when we listen with "raptured ear" and say, with Coleridge :

" 'Tis the merry nightingale
That crowds and hurries and precipitates
With thick fast warble his delicious notes,
As he were fearful that an April night
Would be too short for him to utter forth
His love-chant, and disburden his full soul
Of all his music."

It is well known that some birds, like the thrush and the lark, have a second time of singing after the silence and the critical moult which follow the breeding season. There are others, like the water-ouzel, the robin, and the wren, which sing even during the winter. It may be permissible to suggest that we are here face to face with evolution in process, that bird-song is here rising on a higher turn of the spiral. It is outlasting the nuptial period, it is overflowing into everyday life, it is expressing *joie de vivre* beyond the confines of sex, expressing success in the great task of happiness.

We should like to say at this point that there is a tendency to exaggerate the sex-impulse so as to exclude other excitements that thrill the organism, such as æsthetic delight. The collections of bright things made by jackdaws and the like cannot be regarded as having any direct connection with sex, and the beautiful objects gathered by the bower-birds are surely enjoyed for their own sake. We must do birds the justice of allowing them some appreciation of the beautiful as something else than an erotic. A good case is mentioned by Forel (1906) : a peahen that had never seen a peacock was introduced to one outside the breeding season. She flew rather than ran to him in the greatest excitement, and circled round him in obvious admiration. He remained quite cold and reserved until the advent of spring brought

them together. Forel thinks that there was no question of any direct sexual excitement (of course "sex" is not an insalable activity); the peahen was simply filled with æsthetic pleasure at the novel sight of such a gorgeous kinsman!

§ 10. RECONSIDERATION OF DARWIN'S THEORY OF SEXUAL SELECTION

Darwin's theory of Sexual Selection is no longer wholly acceptable in the form in which he stated it, but modern criticism has erred in over-destructiveness. In regard to some of the questions involved, the wisest course is probably to suspend judgment until fresh facts, especially of an experimental kind, accumulate. In regard to some other implications, however, it seems possible to meet some of the chief objections by a re-statement in the light of new data.

(A) It was primarily in reference to secondary sex-characters that Darwin suggested his theory of sexual selection. Certain variations, *e.g.* in the improvement of weapons and food-catching apparatus, are favoured by natural selection in the course of the every-day struggle for existence; in the same way, variations which are advantageous in securing mates and consummating sexual reproduction will be favoured by sexual selection.

Darwin began with instances of the importance of masculine vigour and equipment when rival males compete for the possession of the females. "The strongest, and with some species, the best-armed of the males drive away the weaker; and the former would then unite with the more vigorous and better-nourished females, because they are the first to breed. Such vigorous pairs would surely rear a larger number of offspring than the retarded females, which would be compelled to unite with the conquered and less powerful males, supposing the sexes to be numerically equal; and this is all that is wanted to add, in the course of successive generations, to the size, strength, and courage of the males, or to improve their weapons" ("Descent of Man," 2nd ed 1888, vol. i. p. 329).

Now it is plain that forceful competition among rival males for the possession of a female or of several females does not differ in kind from the ordinary struggle for food and foothold, except that it is strictly intra-specific. Darwin pointed out indeed (p. 349) that sexual selection is less rigorous than natural selection; that it is less of a life-and-death affair; that it operates through the unsuccessful males having fewer, less vigorous, or no offspring; and that it is not limited by the general conditions of life; but there is in all this no departure from the natural selection position. This part of the theory, therefore, remains valid to those who regard natural selection as a *vera causa*.

(B) Darwin went on to those characters that are useful in the recognition and capture of the females. When a male excels his neighbours in his capacities for finding, pursuing, and catching the female, sexual selection, he said, again comes into action ("Descent of Man," p. 324). The male moth often finds his mate by the olfactory acuteness of his large antennæ; some small crustaceans recognise the other sex almost instantaneously when there is chance contact in the water; in some fishes, recognition depends on colour and on behaviour; many experiments led Goltz to believe that the male frog distinguishes the female by touch; in birds, visual and auditory impressions count for most; in mammals, the scent is often of chief importance (see S. J. Holmes, "Studies in Animal Behaviour," Boston, 1916, pp. 219-328).

Since correct recognition of the one sex by the other is often of essential importance to the race, it is not surprising to find Darwin saying ("Descent of Man," p. 324): "But in most cases of this kind it is impossible to distinguish between the effects of natural and sexual selection." This part of the theory also remains valid, if one believes in selection at all.

(C) Darwin primarily used the term sexual selection for all cases where sifting occurs in relation not to ordinary nutrition and self-preservation, but to pairing. It was only secondarily that he laid emphasis on the "choice" that the

female is supposed to exercise in reference to rival suitors. An interesting confusion, which has misled some biologists, has arisen by a double use of the word selection. Darwin spoke of the female's selection, but it is perfectly clear that he recognised a large field of sexual selection in which there was no question of selection or choice on the part of the female (see "Descent of Man," 2nd ed. 1888, vol. i. p. 323, footnote). Sexual selection meant, for Darwin, sifting in connection with mating, whether the female held the sieve or not.

(D) In his next step Darwin used the word selection in a non-metaphorical sense: "Just as man can give beauty, according to his standard of taste, to his male poultry, or more strictly can modify the beauty originally acquired by the parent species . . . so it appears that female birds in a state of nature, have by a long selection of the more attractive males, added to their beauty or other attractive qualities" ("Descent of Man," 2nd ed. 1888, vol. i. p. 326).

In many animals, at diverse levels of organisation, there is an elaborate courtship-ceremonial, allied, according to Groos, to play. It is sometimes on both sides; it is usually for the most part on the male's side. It includes a manifold display of decorations, colours, agility, and vocal powers. Darwin's theory in this connection was simply this: if there are rival males, and if they are unequally endowed with structural and emotional equipment, or with the capacity of using this to advantage, there will be preferential mating on the female's part, and, other things equal, there will be a selection of the type of male most successful as a suitor. It is the female who sifts, but the logic of the process is the same as in ordinary natural selection.

(E) It is conceivable that pronounced and persistent preferential mating might lead not merely to the establishment and augmentation of characters determining the result of the contest or the courtship, but also to a process of physiological and psychological "isolation" (narrowing of the range of intercrossing), and thus to an accentuation of the apartness of a species as regards crossing with related neighbour-

species (see Karl Pearson, "Grammar of Science," 2nd ed. 1900, p. 418).

(F) At this point attention may be directed to the important contributions to the natural history of mating to be found in H. Eliot Howard's monumental "British Warblers" (1907-1915). We venture to think that this acute and sympathetic observer exaggerates the instinctive at the expense of the intelligent element in the behaviour of birds, and that he is unnecessarily antagonistic to Darwin's theory of sexual selection, but his work is a rich treasure-house of reliable data. It is of great interest, for instance, to discover how much competition there is among the male warblers, before the females arrive on the scene, in the way of discovering and securely holding the most advantageous territories for nesting. Not less important is the evidence that the soberly coloured warblers do not fall behind brilliantly coloured birds in the elaborateness and abandon of their display attitudes and poses. The importance of Bird Territories has been recently emphasised by Mr. Howard in a separate volume (1921).

(G) Darwin was well aware of many of the difficulties besetting his theory. With his wonted candour he anticipated various objections, *e.g.* that the theory "implies powers of discrimination and taste on the part of the female which at first appear extremely improbable" ("Descent of Man," p. 326). The first very serious criticism came from Wallace in 1871, and was restated in his "Darwinism" in 1889. The most elaborate criticism as yet is surely to be found in T. H. Morgan's "Evolution and Adaptation" (1903), where no fewer than twenty-four reasons are given for rejecting the theory. Within our narrow limits we must confine our attention to the three criticisms which seem most important.

There is, in the first place, an admitted difficulty in the scarcity of direct evidence that some of the males are actually disqualified and left unmated. If all the males get mates sooner or later, then no discriminate elimination is effected. Professor Karl Pearson has given statistical evidence of preferential mating in mankind, but this is hardly procurable

in the animal world. Darwin met the objection in various ways. He pointed out that in some species the males outnumber the females, and that in some other species there is polygamy. If the more attractive males have in such cases an advantage in mating, the direction of evolutionary movement will be determined by them, and not by the handicapped residue of the unattractive. He also pointed out that the more vigorous and more attractive males would be accepted by the more vigorous females which are the first to breed, and this would imply a cumulative preponderance of the more vigorous and more attractive types. Even earlier hatching of the young birds might be of critical moment.

As a matter of fact, definite information as to the elimination of some of the males is by no means wholly lacking. Thus in diagrammatic illustration we may refer to some spiders where, as the Peckhams and others have shown, the female sometimes kills a suitor who does not adequately please her. That she may also kill a successful suitor is immaterial, since the mating has been accomplished (see G. W. and E. G. Peckham, "Observations on Sexual Selection in Spiders of the family Attidæ," Milwaukee, 1889, p. 60).

As regards birds, Meisenheimer gives some good instances in his important work on sex (1921, p. 766). A silver pheasant that was for a while a prime favourite went literally "off colour," and then a rival took his place. A captive female of a weaver-bird (*Sporæginthus amandava*) always gave the preference to the male with the most brilliant red, and a female linnæ in the same conditions always chose the male with the brightest crimson on his breast. A similar preference was clearly exhibited by one of the Tanagers (*Pyranga rubra*) which was the subject of experiment. It seems to us that the reality of preferential mating has been satisfactorily proved in certain cases.

In the second place, many critics have objected to crediting the female organism—whether bird or butterfly—with the power of "choice," and while comparative psychology

has not advanced far enough to admit of many definite statements as to the subjective aspect of animal courtship, it may be granted that there is not in the "choice" of any female animal much that would correspond to a human weighing of pros and cons. But the point of importance is whether the mating is in any real way selective, preferential, discriminative. It has been proved experimentally that insects as well as birds may be selective in their eating: is the same true as regards their mating? Even if one adopts the modern view that the female does not choose the "best" out of a bunch of suitors, but rather remains unresponsive to the solicitations of males who do not raise her emotional interest to the requisite pitch, that is quite enough for the purposes of the theory; and it is in agreement with Darwin's own remark about the female bird: "it is not probable that she consciously deliberates: but she is most excited or attracted by the most beautiful, or melodious, or gallant males."

A third objection is more serious. It is one thing to admit the reality of a somewhat vague preferential mating, it is quite another thing to credit the female animal with a capacity for appreciating slight differences in decorativeness or musical talent or lithesomeness. Wallace's statement of this objection is well known. Referring to Darwin's four chapters in "The Descent of Man," he says: "Any one who reads these most interesting chapters will admit that the fact of display is demonstrated; and it may also be admitted, as highly probable, that the female is pleased or excited by the display. But it by no means follows that slight differences in the shape, pattern, or colours of the ornamental plumes are what lead a female to give the preference to one male over another; still less that all the females of a species, or the great majority of them, over a wide area of country, and for many successive generations, prefer exactly the same modification of the colour or ornament" ("Darwinism," 1899, p. 285).

But the edge has been taken off this objection by Lloyd Morgan and others, who point out the gratuitousness of

crediting the hen bird with a standard of taste or capacity for æsthetic valuation. "The chick selects the worm that excites the strongest impulse to pick it up and eat it. So, too, the hen selects that mate which by his song or otherwise excites in greatest degree the mating impulse. Stripped of all its unnecessary æsthetic surplusage, the hypothesis of sexual selection suggests that the accepted mate is the one that most strongly evokes the pairing instinct" ("Habit and Instinct," 1896, p. 217).

It may be insisted, however, that if individual excellence in attractive characters (such as plumes, singing power, dancing agility) does not appeal to the female, it cannot be determinative in preferential mating, and therefore its establishment cannot be effected by any process of sexual selection. Unless the female is somehow aware of the individual variation in question, the theory breaks down, and yet it is difficult to believe that the female is so meticulous in fastidiousness, so detailed in her preferential excitability.

The answer, probably sound, is that the details count, not as such, but as contributory to a general impression. Each has its effect, but synthetically, not analytically. "Even when the female seems to choose some slight improvement in colour or song or dance, the probability is that she is simply surrendering herself to the male whose *tout ensemble* has most successfully excited her sexual interest" (Geddes and Thomson, "Evolution," 1911, p. 172).

(H) If one provisionally accepts the theory that a secondary sex-character may have been established and augmented because it contributed to a decision in preferential mating, one has to face the further question of the significance or racial justification of the courtship-habits—often so prolonged, elaborate, and exhausting. The sifting probably works well in keeping up a standard of racial fitness, for the most persuasive male is likely to be, among animals, the fittest all round. But there is surely more than this.

To Groos and to Julian S. Huxley we owe two luminous suggestions. In his "Play of Animals" (Eng. trans. 1900, p. 242), Groos suggests that "in order to preserve the

species the discharge of the sexual function must be rendered difficult, since the impulse to it is so powerful that without some such arrest it might easily become prejudicial to that end. This very strength of impulse is itself necessary to the preservation of the species ; but, on the other hand, dams must be opposed to the impetuous stream, lest the impulse expend itself before it is made effectual, or the mothers of the race be robbed of their strength, to the detriment of their offspring. . . . The most important factor in maintaining this necessary check is the coyness of the female ; coquetry is the conflict between natural impulse and coyness, and the male's part is to overcome the latter " (*op. cit.* p. 243).

It is very desirable that there should be a fresh study of courtship ceremonies and a reconsideration of Darwin's theory of Sexual Selections in the light of comparative psychology. We have already referred to Julian Huxley's study of the Great Crested Grebe where the elaborate, even self-exhausting, ritual does not directly lead on to coition. We venture to quote again Huxley's general conclusion : " Birds have obviously got to a pitch where their psychological states play an important part in their lives. Thus, if a method is to be devised for keeping two birds together, provision will have to be made for an interplay of consciousness, or emotion between them." The courtship is justified by the strength of the emotional bond it establishes.

The establishment of sexual reproduction and sex dimorphism had many more or less immediate rewards : it meant more economical means of continuing the race ; it was a device for securing the persistence of a successful genetic constitution and for screening the offspring from disadvantageous modifications of the parent's body ; it implied more opportunities for re-arrangements of the hereditary items at the beginning of each new life. The separation of sperm-producers (or males) and egg-producers (or females), differing deeply in constitution, would also tend to increase the possible range of cross-fertilisation, which is often advantageous, and would permit of a profitable division of

labour between the two parents in their relations to the offspring; and so on. But at a great distance the sex-divergence attained another justification; it became the basis of love, it served as a liberator and educator of emotions which have enriched and ennobled the lives of many creatures. As Darwin clearly recognised, characters which were primarily selected in relation to mating might become secondarily diverted by a function-change to even wider issues.

In his "Studies in Animal Behaviour" (1916) Mr. S. J. Holmes has an interesting chapter on the rôle of sex in the evolution of mind. "The primary function of the vocal apparatus of the vertebrates was probably to furnish a sex-call, as is now its exclusive function in the Amphibia. Only later and secondarily did the voice come to be employed in protecting and fostering the young, and as a means of social communication. And the evolution of the voice in vertebrates doubtless influenced to a marked degree the evolution of the sense of hearing. It is not improbable, therefore, that the evolution of the voice, with all its tremendous consequences in regard to the evolution of mind, is an outgrowth of the differentiation of sex." There can be little doubt that the biology of the future will attach not less but more importance to sexual selection. For it seems likely that characters and qualities originally established in this way have often influenced both body and behaviour in reaches now more or less remote from the tides of sex-impulses.

§ 11. SEX-CHARACTERS

Since the beginning of the twentieth century the difficult problem of the origin, evolution and development of sex-characters has been illumined by a series of brilliant experimental researches, which have made reconsideration imperative. This has been facilitated by the masterly work of Kammerer ("Ursprung der Geschlechtsunterschiede," 1912).

A. Sex Differences.—It is usual to classify the differences between the sexes as "primary" and "secondary." The

“ primary ” differences refer to the reproductive organs, the “ secondary ” to those in other parts of the body, such as the larynx or the hair. It is clearer to follow Poll, Kammerer and others in recognising (I.) essential or gonadial differences which must be present if there are sexes at all—the differences between ovaries and spermaries ; and (II.) accessory differences which may or may not be present, some of them subsidiary to the reproductive organs, either internally or externally, and others affecting extra-genital parts of the body. The scheme of division, slightly modified from Poll’s and Kammerer’s, may be thus expressed :

- I. Essential or Gonadial In the reproductive organs proper.
- II. Accessory or Incidental:—
 - (a) subsidiary to the gonads:—either internally, as in accessory glands ; or externally, as in pairing organs, egg-laying organs.
 - (b) somatic or extra-genital:—either internally, as in vocal organs ; or externally, as in colour, hair, feathers, etc.

The sex differences have a structural and a functional side, a morphological and a physiological aspect, but for practical purposes one side may often be disregarded. Thus a chitinous decoration on a male beetle has no vital activity after it is formed ; it is the structural side that is important. On the other hand, the differences in the blood of a male and a female, which are of great importance, may not have any detectable structural expression. Similarly, there are many subtle differences in instincts and impulses, in physiological habit and length of life, which are very real though we cannot say much about their structural expression !

Another consideration to be kept in mind in the classification of sex differences is the degree of permanence in their expression. An adult peacock can never be confused with a peahen, but there are many birds, *e.g.* some ducks, which show great dissimilarity between the sexes at the breeding season and great similarity at other times. In many fishes, such as sticklebacks, the males are conspicuously different from the females at the breeding time, but inconspicuously different at other times. In short, there are many nuptial characters which wax and wane according to the sexual state of the organism.

B. Illustrations of Sex-Characters.—Convenient surveys of sex differences are to be found in Darwin's "Descent of Man" and Cunningham's "Sexual Dimorphism." Among Mammals one recalls the gorilla's sagittal crest, the mandrill's enormous canines, the elephant-seal's nasal proboscis, the lion's mane, the narwhal's tusk, the stag's antlers, the duckmole's spur. Among Birds one recalls the peacock's tail, the wing-feathers of the Argus Pheasant, the decorations of birds of paradise and humming-birds, the tail of the lyre-bird, the neck-feathers of the ruff, the cock's spur, the great bustard's inflatable throat pouch. In some parrots the female is red and the male green! Among reptiles there are a few cases like the erectile dorsal crest of *Anolis cristatus* and the bony horns of some chamæleons. Among amphibians there are the dorsal crests of some newts, the swollen first fingers of frogs and toads, the resonating sacs of some frogs. Among fishes, we recall the salmon's hooked lower jaw, the brilliant colouring of the male dragonet, the "claspers" of Selachians. Among Invertebrates, there are well-known contrasts between the sexes in the Argonaut, in the Giant Japanese crab, in many spiders, in Dynastid and Lucanid beetles, and in many Lepidoptera.

In most cases the positive character is on the male side. He has an extra something which the female does not possess in a developed state, if at all. It is important therefore to recall two or three examples of the converse. The females of the frog genus *Nototrema* have a pocket on the back into which the male pushes the eggs. So far as we know the marsupium of Marsupialia is never more than a rudiment in the males. In the Red Necked Phalarope the female is the more decorative bird. The same is true of the Painted Snipe (*Rhynchæa capensis*), a bird widespread in Ethiopian and Indian regions. It is the female who is the handsomer, and it is interesting to notice that the male, as in the case of Phalaropes, performs most of the duties of incubation.

In some cases the female bird is the larger, and this may

be interpreted in terms of the theory that she has a relatively more anabolic constitution, and in terms of the fact that she has to produce the eggs. Both interpretations require careful handling since the two sexes are usually of approximately the same size, and the male is often the larger. Hilzheimer notes for the male Gos-Hawk a length of 50-55 centimetres, for the female 36-40; for the weight of the male Sparrow Hawk 150 grams, for the female 300 grams; and many similar figures might be cited. But approximate equality is very common.

After a survey of sex-characters, it is well to remind ourselves that conspicuous difference between the sexes is the exception, and general similarity the rule. In many of the higher animals the males and females are very like one another in external appearance. Cat, mouse, rabbit, and hare may be mentioned among mammals; rooks, kingfishers, and many parrots among birds. Below the level of crustaceans, in animals like starfishes and sea-urchins, marine worms, thread-worms, jellyfish and corals, it is rare to find more than minute sex-dimorphism.

Contrariwise, although there may not be any marked dimorphism, there may be a profound functional difference. There are many facts, long since alluded to in "The Evolution of Sex" (1889), which go to show that in their metabolism the male and the female are very different. They run at different physiological rates; the metabolism of the male is relatively more intense. The ratio of katabolism to anabolism is greater in the male than in the female. We may quote a few sentences from another biologist, who seems to take the same view. In his "Sex Antagonism" (1913), Mr. Walter Heape writes: "The Male and the Female individual may be compared in various ways with the spermatozoon and ovum. The Male is active and roaming, he hunts for his partner and is an expender of energy; the Female is passive, sedentary, one who waits for her partner and is a conserver of energy."

Perhaps the average differences between the sexes may be summed up tentatively in this tabular contrast:

MALE.	FEMALE.
Sperm-producer	Egg-producer
With less expensive reproduction	With much more expensive reproduction
More intense metabolism	Less intense metabolism
Relatively more katabolic	Relatively more anabolic
Often with shorter life	Often with longer life
Often smaller	Often larger
Often more brilliantly coloured and more decorative	Often quieter in colour and plainer in decoration
Rising to more intense outbursts of energy	Capable of more patient endurance
More impetuous and experimental	More persistent and conservative
More divergent from the youthful type	Nearer the youthful type
Often more variable	Often less variable
Making more of sex-gratification	Making more of the family

Sex-Characters in Birds.—Turning to birds more particularly we may cite a number of representative illustrations of sex dimorphism, referring for further detail to Darwin's "Descent of Man," Cunningham (1900), and Meisenheimer (1921). The climax is to be found among Birds of Paradise (Paradiseidæ), Humming-Birds (Trochilidæ), and Game-birds (Phasianidæ).

Among Birds of Paradise the females are more or less soberly coloured, the males are resplendent and show specially exaggerated feathers which are erected and often vibrated. The males often congregate in a tree and hold what the natives call a dancing party. "In the Great Bird of Paradise, *Paradisea apoda*, which is found mostly in the Aru Islands, the chief ornament is the great bunch of long and delicate plumes on each flank. These plumes are of an intense golden-orange colour, changing at the tips into pale brown, and are sometimes two feet in length. When erected and made to vibrate, they form a sort of golden fountain almost concealing the body of the bird. In the female all the ornamental plumes are wanting, and the colour is a uniform coffee-brown" (Cunningham, 1900, p. 139).

Among humming-birds, again, the males are usually very much more resplendent than the females. The decorations take the form of tufts which can be erected, of greatly

PLATE VI



BIRDS OF PARADISE (*Paradisaea minor*).
The gorgeous male below, the plain female above.

elongated, often peculiarly shaped, feathers which are displayed, and of brilliant coloration which depends largely on the physical structure of the surface of the feathers. In his "Naturalist in Nicaragua," Belt described the behaviour of two males belonging to the species *Florisuga mellivora*, which were displaying before a female sitting on a branch. First one and then the other shot up into the air and descended slowly with the white tail so much expanded that it covered more space than the rest of the bird. Darwin mentions the interesting case of *Aithurus polytmus*, where the male has brilliant coloration and two immensely long tail-feathers, both characters appearing in the young bird.

The dimorphism of Game-birds is familiarly illustrated in the case of the common cock and hen, and what we see in the poultry yard has its counterpart in the ancestral Jungle-fowl (*Gallus bankiva*) of India. The cock is distinguished by longer tail-feathers, longer and brighter neck feathers, larger comb and wattles, and a spur on the inside of each leg. He is polygynous and combative, and he does not share in the care of the young. Mr. Cunningham refers the elongation of the tail-feathers to their movements in courtship, the elongation of the neck hackles to their erection in fighting, the vascular comb and wattles to pecking by the beaks of other birds, and the spur to the doughty blows delivered on the legs and heads of rivals. As we shall afterwards explain, there are many difficulties, to our mind insuperable, in the way of this direct Lamarckism. We regard all these dimorphic features as the outcome of germinal variations and their subtle sifting.

In birds the sex dimorphism is mainly concerned with plumage and such skin out-growths as combs and wattles, but the variety is nevertheless extraordinary. From the long list we may select a few examples. The male sheldrake (*Tadorna tadorna*) has a red knob at the base of the bill, unrepresented in the female, and at the same place the male Wattle-Duck of Brazil, *Sarcidiornis carunculata*, has a black comb or caruncle, enlarged at the breeding season and absent from the female. The male Tragopan pheasant

(*Cerionis*) has a fleshy blue horn above each eye and a large gular wattle. In his courting excitement he erects the horn and inflates the wattle. In the male Tanagers of the genus *Procnias*, inhabiting wooded country in Tropical America, there are long thread-like or papilla-like outgrowths of skin on the forehead and on the root of the bill (see Meisenheimer, 1921, p. 448).

As to plumage, we may think of the peacock's crown and of the exuberant exaggeration of the tail-coverts which conceal the true tail-feathers or rectrices. There may be crests, ear-tufts, ruffs, neck-capes, hackles, breast-bristles, and so on, in most cases absent or unrepresented in the females. The pigmentation may be different in the two sexes, but in many cases the difference is not so great as it seems, for it is largely due to the physical structure of the surface of the feather. Very common is the elongation and specialisation of certain tail-feathers, sometimes only two, which may consist almost wholly of a very long rachis or may have an expanded decorative disc at the end of this. A very extraordinary case is seen in four-year-old male Lyre-birds (*Menurus*) which have "the exterior pair of feathers curved like a lyre, with very narrow outer and very broad inner webs; the next six pairs have very distant barbs and no barbules, except towards the base; while the two median plumes have narrow inner and no outer webs, and after crossing below, curve boldly outwards. The female has a long, broad, normal tail, the median feathers exceeding the rest" (Evans, 1899, p. 491). In ordinary daily life, the cock keeps his tail horizontal; in his courtship excitement it is erected and the wings droop. As he struts and pirouettes, he sings. He appears to be monogamous.

In the male weaver-birds of the genus *Vidua* and some related genera the four median feathers of the tail are greatly elongated, but while they are broadened in some species they taper to threads in others, or they may have a bare shaft and a "racquet" tip. In another weaver-bird, *Pyromelæna franciscana*, the male puts on at the breeding season a velvety "wedding garment," partly black and

partly scarlet, while during the rest of the year he wears a plain, somewhat sparrow-like suit, as the female always does.

An interesting point is that the transformation of feathers occurs in the less essential tail-feathers much more frequently than in the more important wing-feathers. But there are many instances in this part of the plumage as well. Thus in the extraordinarily decorative Quezal (*Pharomacrus mocinno*) of the Guatemala forests, the male has much elongated wing-coverts, as well as greatly exaggerated and very gorgeous tail-coverts and a high crest. In some of the African goat-suckers of the genus *Macrodipteryx* there is a great elongation of a primary feather or of three of them; in one species the ninth primary is over two feet in length, more than twice as long as the bird's body.

C. Theories of Sex Dimorphism.—*Darwin's Theory.*—

As every one knows, Darwin argued that the evolution of dimorphic sex-characters might be accounted for in terms of selection—especially sexual selection. This has two modes: the combats between rival males and the preferential mating where the female chooses or seems to choose. It must be admitted that Darwin's theory has to face some serious difficulties. (a) What is known experimentally in regard to selective breeding, *e.g.* Johannsen's work, does not favour the view that the level of differentiation of, say, the stag's antlers and the decorations of the bird of paradise could be gradually raised generation after generation by such selection as combats and preferential mating respectively afford. (b) In some cases of pronounced sex dimorphism there is no evidence either of preferential mating or of combats, and subsidiary hypotheses have to be invoked. Thus we have Günther's suggestion that masculine characters have their justification as a means of "bluffing" enemies. (c) Statements in regard to serious disproportion in the number of the two sexes must be taken critically, having broken down in several cases. And it is plain that the value of the selectionist interpretation depends largely on the evidence that considerable numbers of the less attractive or

less well-equipped males are either left unmated, or have less numerous and successful families as the result of their matings. (*d*) As Darwin himself hinted, there is much reason to think that the female who has to be wooed surrenders herself not to the male who has a particular character in special excellence, but to the one whose *tout ensemble* has most successfully excited her sexual interest.

Cunningham's Theory.—In his interesting “Sexual Dimorphism” Mr. J. T. Cunningham argues in support of a Lamarckian interpretation. “In either sex unisexual characters have, as a general rule, some function or importance in the special habits or conditions of life of the sex in which they occur.” “But the important truth, which appears to have been generally overlooked, is that in the case of each special organ its special employment subjects it to special, usually mechanical, irritation or stimulation, to which other organs of the body are not subjected. Every naturalist and every physiologist admits that in the individual any irritation or stimulation regularly repeated produces some definite physiological effect, some local and special change of tissue in the way of either growth or absorption, enlargement or decrease, or change of shape. Thus not only hypothetically at some former time, but actually at present in every individual, the unisexual organs or appendages are subjected in their functional activity to special strains, impacts, and pressures, that is, to stimulation, which must and does have some physiological effect on their development and mode of growth.” To explain the restriction of sex-characters to one sex, to the period of maturity, and often to one period of the year, Cunningham supposed that “heredity causes the development of acquired characters for the most part only in that period of life and in that class of individuals in which they were originally acquired.” Unisexual characters are largely of the nature of excrescences which originated from mechanical or other irritation in the male or the female at particular times and in particular states of body. They are now part and parcel of the inheritance, but they are not expressed in the body except in association with physiological

conditions the same as those under which they were originally produced.

Cunningham seeks to show that sex-characters may be interpreted as the hereditary outcome of special irritations. The legitimacy of this interpretation depends (1) on the experimental evidence that can be adduced to show the origin of callosities, excrescences, proliferations, etc., as the direct result of stimulation, and (2) on the case that can be made out, on experimental or logical grounds, for believing that somatic modifications may be directly transmitted, in some degree at least. This raises the whole question of the transmission of somatic modifications, which we waive. We simply express our opinion, argued for elsewhere, that the evidence does not warrant an acceptance of Cunningham's theory.

With special reference to birds, Cunningham emphasises the connection between erecting the decorative feathers during sexual excitement and the exaggerated growth of these feathers. "The feather is erected by muscular action; the quill of the feather is a hard, rigid body, implanted in a socket in the living skin; and the growth of the feather is due to the growth of the living cells which form the papilla at the base of the feather. The habitual erection of feathers is, therefore, a constant source of irritation of the papilla, and there can be no doubt that the effect of such irritation must be, and is, to cause the feather to grow larger. If it be urged that the feather ceases its growth after a certain time, I would reply that the irritation either acts before growth has ceased, or else produces its effect on the succeeding feather when the first is shed" (1900, p. 109).

"The male, when in the beginning he is quite similar to the female, erects and moves some part of his plumage under the influence of sexual excitement. When he fights he erects his neck feathers partly to ward off the blows of his enemy's beak. When he courts he erects or vibrates other feathers. Nearly all the feathers of a bird can be voluntarily moved or erected. The particular feathers

which the male moves when sexually excited depends on the peculiarities of the species previously evolved, and its habits in ordinary life. Thus a flying bird will fly about when courting, like a humming-bird; a ground bird will strut like a peacock. The male, when he has no voice like that of a singing bird, moves about and agitates his feathers, partly because his excitement finds vent that way, partly to show the female what he desires. Thus for each species particular gestures and erection of particular feathers become habitual, and if the male bird, from his polygamous habits and entire freedom from the cares of incubation or nursing, devotes himself with increasing energy to the practice of these special gestures and movements, the result will in course of time be visible in the corresponding excessive growth and development of the feathers and organs stimulated" (1900, p. 111).

This is an ingenious theory, deserving careful consideration, and we may call attention to some difficulties. (1) It must be noted that the male's peculiarities are often sharply defined, such as the elongation of the ninth primary feathers in an African Night-jar (*Macrodipteryx*) to a length of twenty-six inches, or the great elongation and terminal expansion of two tail feathers in a Bird of Paradise. Is it easy to suppose an erection so precise that it specially stimulates the growth of two feathers in a group? (2) Is it so certain as Cunningham indicates, that the erection of a feather must stimulate its growth, or the growth of its successor? (3) In many birds the reproductive period is sharply punctuated, and the courting behaviour begins suddenly when the feathers are fully formed. (4) It is not merely a question of exaggerated growth of the feathers used in display; in many cases there are marked differences in physical structure and in pigmentation. (5) The correlation between the hormones from the testes and the assumption of the decorative plumage is certain; this does not seem to us to harmonise well with the view that the excessive growth is due to energetic practice in special gestures. (6) The theory involves an acceptance of the hypothesis that individually acquired

functional modifications can be hereditarily entailed in some representative degree.

Surplusage Theory.—Hesse and Doflein have made the interesting suggestion that as reproduction is very much less expensive in the males, they have surplus material at their disposal which may account for their frequently greater variability, for certain characteristics of habit and temperament, and for their exuberant growths of various sorts.

Thus it is said of some humming-birds that the males spend much of their time at the breeding season in fighting and dancing, that they do not share in nest-building, brooding, or feeding the young, that they play while the females work. But it is easy to cite other cases where the male birds do play a large part in the discharge of parental duties.

To the objection that the male is often much smaller than the female, and that his nutritive income will be proportionally less, the answer is given that the decisive fact is one of ratio, *e.g.* between the amount of material expended in reproduction and the weight of the body in the two sexes, or between the size of the reproductive organs and the size of the body in the two sexes.

In cases where the sexes expend approximately equal amounts of material in reproduction, almost no sex-differences occur. Thus in many fishes, such as the herring, the ovaries and testes are about the same size and enormous quantities of milt are shed by the males in the water. In the viviparous Cyprinodonts, on the other hand, where there is internal fertilisation and economy of sperm-material, the males show both permanent and periodic distinguishing features.

In his critique of the surplusage theory, Kammerer indicates some serious, and indeed fatal, objections. (*a*) It may explain how the male has a good deal to spend on decoration, but it sheds no light on the specific line that his expenditure takes—a mane for the lion and antlers for the stag. (*b*) It is easy to pick out cases that suit the theory, but what of the broad fact that in hundreds of cases among birds and mammals, reptiles and insects, the two sexes are equal

in size, equal in numbers, and uniform in appearance, although the expenditure on the male's side is very much less than the female's. (c) The female's reproduction is more expensive, but yet it is the female that tends to fatten. And why is it that when her reproductive expenditure is over, her accessory sex-characters do not improve (except in rare cases), but become less marked than ever? (d) There are many cases where the male has to fertilise the eggs of many females, and where he has no masculine peculiarities, which is what the theory would suggest. But there are also many cases of a similar sort, where the polygamous male, like peacock, pheasant, stag, bull, sea-lion, shows an exuberance of masculine features. Indeed it has been suggested that increased sexual function in the male tends to increase the masculine features, and *vice versa*.

D. Sex-Characters and Specific Characters.—Tandler and Kammerer have done good service in showing that sex-characters behave like ordinary specific characters, *e.g.* in inheritance, in regeneration, and in their relation to environmental influence. We think, however, that they have exaggerated a useful idea, so that in its generalised expression it becomes untenable. Tandler says: "All secondary sex-characters were indeed at first specific characters . . . and not primarily associated with the genital sphere." Thus the milk-gland has doubtless arisen from a group of skin-glands, common to both sexes. Later on, in the female, it came into the service of another function, and under the influence of the reproductive organs. But there is no enigma in its representation in the males.

In Bovidæ the possession of horns is a constant character of a given species or variety. They are present in both sexes. The shape-differences between them form the sex-character. When there is early castration, the two sexes have the same kind of horn, which bears a marked resemblance to the ancestral type of *Bos primigenius*.

According to many authorities, antlers began as variations on the part of the male Cervidæ; they necessarily became

part of the inheritance of the females as well ; but they could not find expression, so to speak, in the female constitution. According to Tandler, however, they were originally possessed by both sexes, like the horns of cattle, and have in the course of time become sex-linked characters, normally developed in the males only, except in the old-fashioned reindeer where they occur on both sexes.

Kammerer comes to the same conclusion : " The sex-characters simply form a particular group of species-characters : all sex-characters are at the same time species-characters." Nevertheless, he distinctly favours Möbius's thesis that there is a sort of somatic sex, a sex-differentiation of all the organs and tissues, whether they show a visible difference or not, so that one may, he says, invert the previous sentence and say that all species-characters are also sex-characters. But, in any case, there are certainly no special sex-characters, which stand apart from other species-characters, as things *per se* and autonomous.

In their recent work, " Die biologischen Grundlagen der sekundären Geschlechtscharaktere," 1913, Tandler and Grosz are very emphatic in their conclusion that all sex-characters have been derived from specific characters or " systematic " characters, which in the course of time have been brought (by the usual method of variation and selection) into the service of reproduction. This occurred at different periods, as is suggested by their different degrees of variability to-day. And *pari passu* with their evolution they have come into correlation with the gonadial glands of internal secretion which supply their indispensable liberating stimuli. " The secondary sex-characters are to begin with systematic characters and they ultimately owe their development and differentiation to the harmonious co-operation of the glands of internal secretion."

In some birds there is a spur or weapon developed in the carpal, carpo-metacarpal, or even digital region in both sexes, as in Parra and Hoplopterus, the ducks Merganetta and Plectropterus, and the screamers Palamedea and Chauna. The spur is a specific character, and is used in fighting. If

it should occur in related types in the males only and be used only in their combats, it would illustrate Tandler's theory. And it should be noticed that in the pugnacious extinct Solitaire of Rodriguez there is a walnut-like excrescence (an exostosis) developed on the lower end of the radius and a similar tubercle on the upper end of the carpo-metacarpus—in the males only.

It must be borne in mind that in many cases where the sexes are practically identical, there are special features that appear in mature birds at the breeding season, such as the extra horny plates at the root of the puffin's brightly coloured bill, the white hair-like feathers occurring in the dark plumage of cormorants on head, neck, and shank, the long horny orange-coloured up-growth at the root of the bill in *Chimerina cornuta*, one of the auks of the Bering Sea. In the case last mentioned the process is moulted off—like the puffin's accessory plates—in the autumn, and developed afresh in spring.

The thesis that: "All secondary sex-characters were at first specific characters," appears to us to be an exaggeration of a sound idea. A specific character may be transformed into a secondary sex-character, so that it has a different expression in the two sexes, as when the tail-coverts, present in both peacock and peahen, are transformed into the male's gorgeous tail. But an exclusively male character may arise *de novo*, apart from any previous counterpart among the specific characters. And similarly for an exclusively female character.

There are, it seems to us, *numerous* peculiarities of one sex or the other which cannot be readily derived from specific characters supposed to be common to both sexes. And if it be said that the cases we would adduce are not fair samples of sex-characters, we would reply that it is very difficult to draw a line round "secondary sex-characters," separating them from other sex-differences. This is especially difficult among Invertebrate animals where we have little knowledge of glands of internal secretion connected with the essential gonads, and are therefore bereft of that useful criterion of a

secondary sex-character which has been discovered in Vertebrates.

Let us consider, then, a few striking sex-differences in the light of Tandler's theory. The female Paper-Nutilus (*Argonauta*) is very different from the male. She is much larger, she has two "arms" peculiarly modified to secrete a unique shell, not homologous with other Cephalopod shells, which is used as a brood-chamber for the developing ova. The small male has no such shell and no such modification of two of the arms. When he is sexually mature, one of his arms becomes laden with sperm-packets and is discharged as a "hectocotylus" into the mantle cavity of the female.

These are familiar facts, but we do not know of any evidence for supposing that the immediate ancestors of the Paper-Nutilus had an external shell or modified arms such as the female now shows. There is no hint of such a thing. Moreover, the shell is not for living in, but for the protection of the eggs; it is a cradle not a house, and it has no meaning except in the female.

Among birds we can find some good illustrations. Thus in the Great Bustard, *Otis tarda*, the male, which is considerably larger than the female, is marked by whisker-like plumes on the cheeks and by a great air-pouch opening below the tongue. Neither of these features is to be seen in the female. The throat-pouch is extraordinarily inflated when the male is displaying before the female. It disappears almost or quite completely after the breeding season. But the point is that the sub-lingual pouch must be regarded as a new structure, possessed by the male only, not hinted at in the female. There is no warrant for regarding it as a masculinised specific character.

Let us take one of those very interesting cases where the female has something definite and positive which the male has not—the frog *Nototrema* with its dorsal pouch in which the eggs are carried. Is there any warrant for supposing that this was once a specific character?

Another case in point may be found in the so-called

claspers of male Selachians and Chimæroids. In a fish like the skate they are very conspicuous sex-characters ; they are highly specialised structures with complicated musculature and skeleton. In the Chimæra they are even more complicated. They are very definitely male organs, and in some cases at least they are inserted into the cloaca of the female in the process of sexual union. Phyletically they are specialised portions of the pelvic fins, but there is no trace of them in the female. So far as we know, there is no warrant for supposing that the ancestors of our modern Selachians had in both sexes structures like the claspers.

Similarly, the male spider is often very markedly distinguished from the female not only in size, but by the great complexity of the pedipalps which are used in transferring the sperms into the female. The sex-character here is not the pedipalp, which is of course common to both sexes, but the extraordinary elaboration of the end of this appendage. We do not know of any warrant for regarding this as other than a masculine character.

Again, in most Mammals the testes are carried in an external pouch or scrotum (into which they descend, as if by a normalised rupture, at a certain stage of development), while the ovaries always remain internal. This is a definite male peculiarity, an extra thing that is not hinted at in the female : and we do not know of any warrant for regarding this as a transformation of a specific character once common to the two sexes.

Can Masculine Characters pass to the Female?—In some birds there is an indication of this, and the same is true of many other animals. The point is whether a secondary sex-character, primarily restricted in expression to the male, may find normal occurrence in the female as well—perhaps through some variation in the hormones from the reproductive organs. We know experimentally that the removal of the ovary of a bird may be followed by the development of the masculine plumage, normally inhibited. May not the extension of a masculine character to the female have occurred occasionally in natural evolu-

tion? The reindeer is the only deer with antlers in the female as well as in the male. Is this a case of the extension of an originally masculine character to the female, or does it illustrate Tandler's theory—that antlers primarily occurred in small measure on both sexes, but were gradually suppressed (with the single exception of the reindeer) in the female, and exaggerated in the male? It remains a question of interpretation.

In the peacock-pheasants (Polyplectron) some of the species have plain-coloured females, but in the other species there is an approach to the male splendour. In one of the wild-turkeys (*Meleagris ocellata*) the decorative "eyes" on the tail occur in both sexes. There are not a few of these cases, but it seems difficult to decide whether species-characters are becoming somewhat divergent sex-characters, or whether a character primarily masculine is becoming a species-character of both sexes.

The syrinx or song-box may be regarded as a possession of both sexes, but it often attains to a much stronger and more complex development in the male bird. Thus among ducks the males often show a special enlargement or resonating sac, and Meisenheimer (1921, p. 738) calls attention to the fact that a female Australian widgeon (*Mareca punctata*) is unique in showing in the adult an approximation to what occurs in the male. He regards this as the beginning of an extension of a masculine character to the female, and gives as another example the incipient coiling of the windpipe in some females. It is coiled round several times in many males.

Suggested Theory of the Mode of Origin of Sex-Characters.
—If we turn aside from the hypothesis that sex-characters arose by the hereditary accumulation of the direct results of somatic modifications, whether functional or environmental, we are led to conclude that they arose as germinal variations or mutations. That the germinal origin of variations or of mutations is wrapped in obscurity makes all phylogenetic ætiology difficult; there is no *special* difficulty in regard to sex-characters; the problem of

their origin is probably in essence like that of any other characters.

Without straying far from our present path, we may recall some of the possibilities as regards the origin of variations. The opportunities afforded in maturation and fertilisation may bring about a shuffling of the chromosome cards. Fluctuations in the nutritive stream may bring about changes in the germ-cells. External changes may serve as trigger-pulling variational stimuli to the highly complex germ plasm. There is a tendency in matter to complexify, no more explicable than gravitation, but real; perhaps the living unit utilises this in its *germinal experiments in self-expression*, for that is what we believe mutations, at least, to be.

Let us suppose, then, that a germ-cell already predisposed to develop into a female-producer was the seat of a variation, say in the determinants or factors corresponding to the future ovary. Let us suppose that this variation was in the direction of producing an accessory yolk-gland. In the course of development the determinant or factor, if consistent with the rest of the constitution, is actualised and there is the beginning of a yolk-gland—an advantageous addition obviously. In the course of time the organism reproduces and its germ-cells have entailed on them (in accordance with the conception of germinal continuity) the determinant or factor of a yolk-gland. But the difficulty immediately arises in the mind that this new hereditary item will be found not only in the germ-cells which will develop into females (where it will be relevant), but also in the germ-cells which will develop into males (where it will be irrelevant). What then will happen to the yolk-gland determinant in those germ-cells that are going to develop into males? The answer is that it will remain latent, not because its expression would be irrelevant, which is a finalistic idea, but because it arose as a variation in a gamete predisposed to develop into a female. It is solidary with femaleness, which, for us, means a metabolism-ratio or rhythm with relatively preponderant anabolism. Metaphorically, it is a seed which

will germinate in female soil, which will not germinate in male soil, though it will remain latent there.

For the sake of clearness, let us take the same occurrence on the male side. In a germ-cell (whether ovum or spermatozoon or fertilised ovum) predisposed to develop into a sperm-producer, a variation arises, say, in the direction of brilliant pigmentation of the skin. If it is consistent with the rest of the organisation, it is realised in development; it is a success; all the spermatozoa have it, and it is transferred to a multitude of ova. But it develops only in those fertilised ova which are going to develop into males. It does so develop because it was, to begin with, a variation—a new departure—made by a male-producing gamete. It is a seed which can germinate only in a male soil, which will remain latent in a female soil. Thus a germinal variation in the parthenogenetic ova of the bee which develop into drones, will be unexpressed in the queens, but none the less faithfully handed on by them.

In the case of birds, the spur of a cock, the lingual-pouch of a bustard, the two orange-coloured sacs on the neck of the prairie-cock of North America, the extraordinary rugged excrescence on the radius and carpo-metacarpus of the extinct Dodo, the large resonating bulb associated with the song-box in some drakes (*e.g.* the Eider) may be mentioned as good examples of masculine peculiarities which develop only in masculine "soil." These characters are in a somewhat different category from those where the dimorphism is quantitative, *e.g.* longer feathers. By "soil," let us repeat, we mean the constitutional metabolism, including the secretion of the ductless glands.

We venture then to suggest the hypothesis, that distinctively masculine characters all arose from variations in gametes predisposed or predetermined to develop into males, that distinctively feminine characters all arose from variations in gametes predisposed or predetermined to develop into females, and that this primal difference in origin explains (1) why the new gains are often confined in their expression to one sex, and (2) why they hang together in a hereditary

congeries. The hypothesis is in no wise inconsistent with the view that many sex-characters are transformed species-characters, for the variation in such cases was the transforming. Nor does the hypothesis conflict in the least with the facts in regard to the importance of hormones in the individual development of the sex-characters, that is a question in the physiology of development. Nor does the hypothesis conflict at all with the view that some process of Selection favoured the persistence and diffusion of the new character. The hypothesis concerns the *origin*, not the ontogenetic development, nor the phylogenetic evolution.

One of the arguments that may be used in support of our hypothesis is that used in a slightly different connection in "The Evolution of Sex" (1889). It is this. There are numerous distinctively masculine characters which have some measure of "family resemblance," which look as if they had something in common, which are congruent with the intenser metabolism of the male sex. To a thorough-going Lamarckian this is readily intelligible, for he regards the colour-display, the exuberance of integumentary out-growths, the erection of parts of the body such as crests and tail-feathers, the growth of weapons on the one hand and embracing organs on the other, as natural developments of the intensely living, lusty male, as natural individual developments, whose results have gradually been incorporated in the heredity-bundle. But we cannot take this view of the matter. We do not believe that Nature works in this *direct* way. Our suggestion is that such measure of congruence as there is in, say, masculine sex-characters (*e.g.* brighter colouring, exuberant decoration, smaller size) may be hypothetically interpreted as due to their having arisen as germinal variations or mutations in germ-cells predetermined to develop into males.

As a subsidiary hypothesis, we venture to suggest that augmentations of the activity of the gonadial glands (due either to germinal or to nurtural causes) may have from time to time set free in the organism an unusual abundance of hormones with a corresponding exaggeration of individual

sex-characters. Now, to those who are Weismannists by conviction, and yet have a suspicion that there must be something in Lamarckism after all, we wish to suggest for critical consideration the hypothesis that this unusual abundance of hormones (of the nature of which very little is known) may exert an influence *on the germ-cells* in the gonads and stimulate in them the determinants corresponding to the secondary sex-characters which are being especially stimulated in the parental body in question.

E. Sex-Characters in Individual Development.—We can imagine that what takes place in ontogeny is somewhat as follows. The fertilised egg-cell, in a way inconceivable to us, is the vehicle of the determinants (or factors, or initiatives, or potentialities !) of all the characters proper to the species. It also contains the possibility of giving rise to the characters peculiar to either sex, whether of the essential sex organs, or of the subsidiary sex organs, or of distant parts of the body. It is probable that whatever determines whether the fertilised egg is to develop into a sperm-producer or an egg-producer at the same time determines that it shall develop the masculine or the feminine set of characters. The cause which determines that the fertilised ovum is going to develop into a peacock with testes, also determines that it is going to develop into a peacock with enormous and decorative tail-coverts.

We may compare the determinants of sex-characters to seeds which will not germinate except in particular kinds of soil. The determination of sex settles the question of (protoplasmic) soil. If the fertilised egg is going to develop into a male all the "masculine seeds" will germinate; if the fertilised egg is going to develop into a female all the "feminine seeds" will germinate. If the sex is imperfectly differentiated, as in casual hermaphrodites, then some features of both sets—masculine and feminine—may find expression.

Darwin noted that female birds (*e.g.* poultry, pheasants, ducks) may put on masculine plumage and some other

masculine characters in old age, or when the ovary is diseased or injured. In modern physiological language, the hormone that inhibits masculinity is no longer operative. Conversely, but more rarely, a castrated male may exhibit feminine characters. Thus Darwin noted that a capon may incubate eggs and bring up the young, and that sterile male hybrids between the pheasant and the fowl may behave in a similar way (see also Marshall, 1910, 315 and 654).

To the question why the fact that the fertilised ovum is going to develop into a male (or a female) should *ipso facto* imply that all the masculine (or the feminine) characters are to find expression, we have given the answer that the characters are all correlated, they are there or not there *en bloc*, they form a sex-linked assemblance. And as a reason for this correlation we have suggested (1) that all masculine (or feminine) characters originally arose as germinal variations in gametes predisposed to develop into males (or females), and (2) that in some cases these variations may be plausibly interpreted as congruent or solidary with the characteristic male (or female) diathesis. And to this there requires to be added the very important consideration that just as a thyroid gland and a pituitary gland have arisen in the course of evolution with most important functions in the internal economy of the organism, so in the course of evolution the gonadial glands have arisen, whose internal secretions, working in harmony with other internal secretions, serve as the liberating stimuli and indirectly as the regulators of the development of the sex-characters.

§ 12. HORMONES AND SEX-CHARACTERS

Modern work has shown that the development of secondary sex-characters has sometimes become linked to the reproductive organs, from which there come internal secretions with stimulating or inhibiting potency. These internal secretions (hormones which excite and chalones which slow down) are carried by the blood from the repro-

ductive organs throughout the body, like chemical keys searching for certain locks which they can open or close. It is not that the gonadial hormones furnish anything towards the production of a structure like a comb or a wattle, they stimulate pre-formed tendencies of growth. They are of the same order as other morphogenetic internal secretions, such as that of the thyroid gland ; and it must be understood that the potency of the gonadial internal secretions is not confined to the secondary sex-characters, it is seen also in relation to habit of body and to general behaviour.

The influence exerted by the gonads on the secondary sex-characters differs in different groups of animals. In insects the development of the secondary sex-characters is independent of the gonads. In male crabs the removal of the testes profoundly changes the composition of the blood and induces the putting on of feminine characters, which is just the reverse of what happens in birds. In Mammals the removal of the testes produces an effect very similar to that seen on the male bird, but the castrated female mammal undergoes little change in her secondary sex-characters.

Goodale's Experiments.—An important series of experiments on Rouen ducks, brown Leghorns, and other birds has been made by H. D. Goodale, 1916.

The plumage of the castrated male is little changed ; but that of the female extensively, as regards shape, size, colour, and colour-patterns of feathers.

The capon's comb and wattles remain rather infantile ; in the castrated hen the comb becomes large and male-like in some, but remains small in others.

The capons have well-developed spurs, and in the castrated hens which put on male plumage there were well-developed spurs. In cases where the assumption of male plumage was partial or temporary (owing to partial removal of the ovary), the spurs which had begun to grow continued doing so after the plumage had reverted. This suggests that the dependence of the spurs upon the internal secretion is relatively slight. The inhibition exerted in the female upon the development of the spurs is so slight that once they

have started to grow the hormone is not always able to check them.

Castrated ducks of both sexes showed no change of voice, but castrated fowls are disinclined to give utterance to any kind of sound. Capons can utter all the sounds of which the cock is capable, but they rarely do so.

As far as Goodale's experiments went, with one exception, the operations left the moult of the capon uninfluenced, but castrated drakes lose the power of developing the summer plumage. The colour of the drake's mandible was unaffected, but in the duck certain pigments disappeared. The behaviour of castrates is on the whole negative as compared with normal adults; it corresponds rather closely to that of young birds shortly before they become mature. The birds eat, drink, and move about rather quietly.

It seems clear that while some secondary sex-characters are absolutely dependent on the internal secretion of the gonad, such as the comb, others are more or less independent, such as the spurs.

If the testes of the bird be removed, the majority of the secondary sex-characters develop, though a few may remain in an infantile condition. Thus "hen-feathered" males illustrate juvenile, rather than female characters of plumage.

If the ovary of a domestic bird be removed completely, many of the secondary sex-characters of the male appear, and always of the male of the same race. Some castrated ducks become nearly complete replicas of the male, others are imperfect imitations. But it is not to be supposed that the female is a suppressed hermaphrodite, it is rather that the male characteristics are latent, and that they find expression on the removal of the ovary, the hormone of which normally keeps them inhibited.

As an abnormal occurrence there is a certain amount of hermaphroditism in birds. A number of cases in fowls, where females with embryonic or degenerating ovary showed some development of testes, as well as external masculine characters, have been described by Alice M. Boring and Raymond Pearl (1918). There is no structural counterpart

for the abnormal behaviour of one hen treading another hen, which is probably due to an assertion of latent masculinity, normally kept in check by the hormone of the ovary.

Secondary sex-characters may differ in their relations to the puberty gland (which produces the gonadial hormones). Thus A. Lipschütz (1917) divides the sex-characters of Vertebrates into two groups: (1) sex-characters not dependent on the puberty gland, but the outcome of the characters of the hypothetical non-sexual embryonic form; in other words, parts of the racial inheritance; and (2) sex-characters dependent on the hormones of the puberty gland, which evoke them by acting on the hypothetical non-sexual embryonic form, either in the way of provocation or of inhibition. A castrated cock develops the characteristic plumage and spurs; which suggests that these two characters are not dependent on the gonadial stimulus. A castrated hen assumes the plumage and spurs of a cock, and Lipschütz's view is that in normal conditions the female gonadial internal secretion changes a possible male-like plumage into a female one and inhibits the growth of the spurs. It appears to us that if the facts are quite correct it would be simpler to say that the factors for spurs, for instance, are parts of the racial inheritance, which find full developmental expression only in a male constitution (hormones included), being inhibited in a female constitution (hormones included).

The transformation that may ensue after the removal of the ovary is sometimes extraordinary. The unsexed female bird may become much more masculine than feminine. Thus C. C. Guthrie (1910) describes a case of a pullet from which the ovary was removed: "The pullet acquired not only the outward anatomical features of a cock—cock's comb, wattles, long hackle and tail feathers, rapidly developing spurs, carriage, etc.—but the behaviour as well was that of a male; it exhibited a pugnacious attitude towards cocks, was attracted to hens, and even went so far as to tread hens as a cock."

Pézard points out (1915) that a capon and a castrated

hen may be almost indistinguishable, being like an ancestral form in which the sex-dimorphism was less marked. The removal of the ovary from the hen allows the spurs and plumage of a cock to grow. The removal of the testes from the capon puts a stop to the development of the comb.

O. Riddle has noted (1914) that female pigeons hatched early in the season (when most males are produced) are more masculine than their sisters hatched late in the season. Now if extracts from the ovary of a pigeon be injected into those masculine females, they come to behave like normal females. Contrariwise, if testicular extract be injected into females that are acting in a normal way, they come to behave as males. This points to the conclusion that the sex-behaviour of a bird is determined by internal secretions from the gonads, and that these are carried by the blood to the central nervous system.

As to the precise source of the hormones that appear to come from the reproductive organs, this is probably to be found in "the interstitial cells" that are always present in the ovary. The difficulty is in regard to the male bird, for the results of good observers are very discrepant. Some declare their presence in the testes, and others, as emphatically, their absence. Some discussion of the conflicting results will be found in a paper by Alice M. Boring and Raymond Pearl (1917). These investigators found in the testes of newly hatched chicks interstitial cells structurally identical with those occurring in the ovary. But these special cells are usually absent in males over six months old which have reached full maturity, in respect of both primary and secondary sex-characters. There is obviously a difficulty here, and more facts are required.

In the ovary of the hen there is a corpus luteum closely resembling that in a mammal like a cow. It forms in the place of discharged or degenerate follicles, and the cells contained a yellow pigment and a fatty substance (Alice M. Boring and Raymond Pearl, 1918). It is believed that hormones pass into the blood from the corpus luteum and are distributed through the body.

§ 13. WHAT DETERMINES SEX ?

Many answers have been given to the question : What determines whether a fertilised egg-cell will develop into a male or a female organism ? But the only answers that can be considered seriously are the following :—

(I.) **Possible Influence of Nurture on the developing Offspring.**—In some organisms the sex seems to remain undecided for some time, and the conditions of “nurture,” *e.g.* diet, seem to sway it to one side or to the other. Thus one of the most instructive of recent biological stories concerns a remarkable green worm called *Bonellia*, which is well known in the Mediterranean. The female has a flask-shaped body an inch or two in length, and a flexible bifid proboscis much longer. The male is very simple in structure, the merest pigmy in size, a hundred times smaller than his mate on whom he lives as a parasite. Now the zoologist Baltzer has shown that if the very young sexually indifferent larvæ of *Bonellia*, just hatched from the eggs, happen to become attached to the proboscis of an adult female, they develop into males ; whereas, if they fail to attach themselves and sink into the sand or mud, they develop slowly into females—with very few exceptions. But the story does not end here. Baltzer helped some of the very young free-swimming *Bonellias* to attach themselves to the proboscis of a full-grown female ; those that he left attached for a very short time developed into almost perfect females ; those that he left attached for a long time became perfect males, if such degenerate pigmies can be called perfect ; while those which he left attached for intermediate periods showed various stages of inter-sex. These fine experiments seem to point to a conception of sex as something constitutional, quantitative, plastic, and even reversible. If the metaphor be permissible, the radical difference between the sexes is one of physiological gearing. In the terminology of “*The Evolution of Sex*” (1889) the ratio of anabolism to katabolism is higher in the female than in the male.

It must be remembered that there are not a few animals

which are first male and then female in the course of their individual life. Thus according to Mr. J. T. Cunningham and Nansen the explorer, who served his scientific apprenticeship as a zoologist, the glutinous hag (*Myxine glutinosa*), a strange antiquity of a creature which lives in deep water in the North Sea and sometimes bores into fishes caught on the fishermen's deep-water lines, is one of these first-male-and-then-female animals. In technical language, it illustrates protandrous dichogamy.

Then there is the remarkable fact that a male shore-crab which has its constitution altered and its testes destroyed by *Sacculina* or some related parasite begins to put on feminine and female characters. The abdomen broadens, its appendages change towards the feminine type, and eggs may be produced. Using the terminology of "The Evolution of Sex," Geoffrey Smith said of the change in the constitution of the male crab: "This adaptive regulation consists in the production of at least a partially female condition of metabolism as opposed to the wholly male condition, the female condition being preponderantly anabolic or conservative, as opposed to the katabolic male condition, and by this change from a katabolic to a more anabolic condition the animal can withstand better the drain on its system increased by the parasite."

Another useful consideration is that the distinction between male and female is not always clear-cut, for in types so different as water-flea, moth, and pigeon, the occurrence of inter-sex individuals is well known.

Experiments on altering the sex of such larvæ as tadpoles and caterpillars by alterations of nurture have not been conclusive because the experimenters have not paid sufficient attention to differential mortality. Yung found that tadpoles, which normally develop into about 57 females to 43 males, yielded, when fed with beef, fish, and frog-flesh, respectively 78, 81, and 92 females in the hundred. But this is inconclusive until we know precisely how many larvæ died, and how many of these showed that they were going to become males.

Darwin estimated the ratio of male chicks to female chicks at 48·64 : 51·36 ; and Professor Raymond Pearl (1917), working on a basis of 22,000 chicks, found the ratio to be 48·57 : 51·43, a very close confirmation. Prenatal mortality in the fowl is not differential in respect to sex, and in consequence the observed sex-ratio at birth is to be regarded as substantially the same as the ratio established in the fertilised eggs. This is not always the case in animals, for male embryos may prove more delicate than females. Professor Pearl points out the great importance of knowing the precise sex-ratio before making deductions in regard to sex-determination. Before changes in the sex-ratio can be regarded as indicative of either environmental effects or hereditary bias to male-production or female-production, it is necessary to show that the changes occur with such frequency as to exceed considerably that expected on the basis of chance alone.

As regards birds, we may almost dismiss the theory that nurture is a directly determining factor. The sex is settled very early in embryonic life, and there is no evidence of an indifferent period. That peculiarities of nurture may operate indirectly will be seen later on.

(II.) Possible Importance of the Relative Condition of the Germ-Cells at Fertilisation.—Many breeders believe that there is significance in the relative ages of the parents at the time of fertilisation, in the relative vigour of the parents, in the relative ages of the germ-cells. Schultze's prolonged experiments with mice gave no support to any of these opinions ; but Hertwig and Kuschakewitsch found that either over-ripeness or under-ripeness of the eggs (due to artificially delaying or hastening fertilisation) led to a large excess of females. Kuschakewitsch, working with ova with a high degree of over-ripeness, actually obtained cultures of male tadpoles only, and with only 4·6 per cent. of deaths. These factors are not known to apply in the case of Birds.

(III.) Are there Pre-determined Male-Producing and Female-Producing Germ Cells?—In the vine-pest *Phylloxera* among insects and in *Hydatina* among Rotifers, there

are large eggs which develop into females, and small ones which develop into males. Both develop without fertilisation, so that in these cases there is no question as to the possible influence of the sperm. In one of the mites (*Pediculopsis*) and in a primitive worm called *Dinophilus*, in both of which fertilisation occurs as usual, there are large egg-cells which develop into females, and small ones which develop into males. Mere size means little, it is probably an index of some constitutional difference in the rhythm of the metabolism.

Such cases as we have mentioned point to the idea that there may be *ab initio* female-producing ova and male-producing ova. This view is corroborated by the fact that "identical twins," which develop from one ovum, are always of the same sex; and the same holds for the quadruplets which one of the armadillos normally produces from one ovum. They are all males or all females. In some of the parasitic Hymenoptera, such as *Encyrtus*, one ovum forms a group of embryos which are always of the same sex—females if the egg be fertilised, males if it be not fertilised.

This leads to the suggestion that the decisive factor in some cases may be the spermatozoon, and it is very significant that in about thirty different kinds of animals there are two kinds of spermatozoa, which differ in details of form, while in many other cases, especially among insects and arachnids, half of the spermatozoa have in their nucleus the same number of nuclear rods or chromosomes as the ova have, while the others have one fewer. When a spermatozoon with the extra or X-chromosome fertilises an ovum which also has the X-element, the result is a female. When a spermatozoon without the X-chromosome fertilises an ovum which has the X-element, the result is a male. It looks as if the presence of two X-elements was necessary for the development of femaleness, whereas the presence of one suffices for the development of maleness.

As regards birds there is considerable evidence that there are two kinds of egg-cells, which differ in the rate or

intensity of their chemical processes, and are respectively male-producing and female-producing.

Riddle's Experiments.—Professor Oscar Riddle has found that the ova of the pigeon are dimorphic. That is to say, there are male-producing ova and female-producing ova, distinguishable from one another.

The male-producing egg of the spring is an egg that stores less material than does the female-producing egg of the autumn. The male-producing egg of a clutch *stores* less material than does its female-producing neighbour. The eggs of old females store more material than do those of birds not so old, and they yield a higher percentage of female offspring.

Thus it is evident that the egg of female-producing tendency is one whose *storage* metabolism is high as compared with the eggs of male-producing tendency. Moreover, the chemical analyses show that during the season successive clutches present eggs with higher and higher storage. The earlier clutches store less and some experiments showed that they tend preponderantly to develop into males. The later clutches all store more, and the same line of experiments showed that they tend preponderantly to develop into females.

The contrast between the two kinds of eggs must be stated more precisely. "The progressive *increase* in *storage* capacity of the eggs during the season—under overwork—is to be interpreted as a decrease in the *oxidising* capacity of these same eggs. Living cells in general dispose of ingested food by storing it or by burning it. If oxidised, the products of the oxidation are removable, and do not serve to increase the bulk of the cell. The *low-storage capacity* of the male-producing eggs, as compared with the *high-storage capacity* of female-producing eggs, is, therefore, an index of *higher oxidising capacity*, or, as more usually stated, a *higher metabolism* of the male-producing eggs as compared with the female-producing eggs." There is also some evidence (with exceptions) that the male-producing ovum has a higher percentage of water than the female-producing ovum, and

this is of interest because the more hydrated state of the colloids favours a higher rate of oxidising metabolism, while the less hydrated state favours increased storage. An estimate of the energy-value of the yolks, determined by the calorimeter, confirms these conclusions as to the fundamental contrast between male-producing and female-producing eggs.

Dr. Riddle's thesis is corroborated by curious facts in regard to sex-behaviour. Thus, females hatched from eggs laid earlier in the season are more masculine in their sex-behaviour than are their own full sisters hatched later in the season. Several grades of females can be arranged in a series according to the season of hatching. The female hatched from the first egg of a clutch is in the majority of cases more masculine than her sister hatched from the second of the clutch. And another curious point is the frequency with which the right ovary persists in birds hatched from eggs otherwise known to be most biased towards femaleness.

It seems that sex and such qualities as fertility and developmental energy not only bear initial relations to the order of the egg in the clutch, but that they can be *progressively modified* under stress of *reproductive overwork*, until at the extreme end of the season certain feminine features are abnormally or unusually accentuated. Thus a hereditary character, such as fertility, may have some degree of plasticity—of quantitative plasticity at least.

The experiments outlined above point to a very important conclusion: that sex is a quantitative modifiable character, associated with modifiable metabolic levels. Femaleness in the egg is associated with low metabolism, lower percentage of water, and higher total of fat and phosphorus, or of phosphatides; and conversely for maleness. Analyses of the blood of adult birds go to show that the metabolic differences of male and female germs are also expressed in the constitution of the adult birds. In the adult female the blood-plasma is richer in alcohol-soluble substance and phosphorus than in the adult male, and this increases during sexual activity.

The agreement between Riddle's experimental results and the interpretations offered by Geddes and Thomson in "The Evolution of Sex" (1889) is remarkable. Dr. Riddle writes: "A general classification of male and female adult animals on the basis of a higher metabolism for the one and a lower for the others, was indeed made by Geddes and Thomson many years ago. It now seems beyond question that this conclusion of these authors is a correct and important one." It should be added that the argument of "The Evolution of Sex" (1889) included some evidence that the determination of sex in the individual was dependent on influences affecting the metabolic level. Conditions favouring an increase of the ratio of anabolic to katabolic process ($\frac{A}{K}$) were held to favour the production of female offspring, or the development of a germ into a female organism. Conversely, when the denominator of the fraction $\frac{A}{K}$ is nearer the numerator in amount, maleness will be favoured.

The general thesis, then, is that male pigeons arise from eggs (yolks) of lesser storage metabolism (small size and higher metabolism) and female pigeons from eggs (yolks) of greater storage metabolism (large size and lower metabolism). An interesting corroboration has been furnished by Riddle (1918). He obtained two cases of identical twins which were both females, and which he argues were developed from eggs of high storage metabolism. The proof of this must be indirect, since the eggs developed; but it was known that the eggs were very large compared with all the others (116 and 134) produced by the particular birds in question. If male identical twins were to be found developing from a very small egg it would be an interesting confirmation. It is suggested that the borders of the blastoderm or embryonic disc will be abnormally raised in extraordinarily large eggs and abnormally lowered in extraordinarily small ones, and that this might be the physical cause of the establishment of two independent foci of development, yielding identical twins.

It is only fair to say that the importance of Riddle's experiments makes it peculiarly necessary to have severe testing. The experiments made by Leon J. Cole and W. F. Kirkpatrick (1915) are not in agreement with those of Riddle. They worked with Tumbler pigeons, and came to the conclusion that the sex is determined according to the laws of chance. They did not find that the first eggs tended to produce males and the second eggs females.

(IV.) **Possible Indirect Influence of Nurture.**—If there be two kinds of ova produced in the ovary, and if differences among the spermatozoa do not affect sex in birds, it is possible that peculiarities of nurture may have an indirect effect by influencing the number of male-producing or female-producing ova in the ovary. There may be a differential elimination going on in the ovary, or it may be that young oocytes (immature egg-cells in the ovary) may be biased by nurlural influences towards becoming male-producing or towards becoming female-producing ova.

The normal ratios of 48·57 per cent. cockerels to 51·43 per cent. pullets seems to be determined by the constitution of the fertilised egg, and not by any environmental factors operating during incubation. But it is possible that it may be modifiable by inducing the production of ova of an anabolic type and also by a change in the laying ability of the hen. For, according to Raymond Pearl (1917), the constitutionally more fecund hens tend to produce a larger proportion of female offspring, and it is possible to breed strains of poultry with high productivity as a fixed characteristic. When the poultry man breeds along the right lines for increased egg production, he will at the same time be producing a strain in which profit-making pullets will preponderate over the less profitable cockerels. It may be suggested that the high productivity is the outcome of a constitution in which the ratio of anabolism to katabolism is relatively high, and that female-producing eggs are the outcome of similar physiological conditions.

Reference may here be made to Heape's breeding experiments (1907) on canaries. In one aviary the con-

ditions were such that they conduced to early breeding, without there being specially rich nutrition. The reproductive functions were "forced" without being richly fed. These birds produced males in great excess. In the other aviary the birds were rather kept back; they nested later and moulted later; their reproductive functions were not stimulated; the ova matured more slowly and were at the same time more highly fed. These birds produced a marked excess of females. It is probable that the environmental differences operated by selective action on the germ-cells produced.

(V.) **Mendelian View of Sex.**—If sex, like many a morphological character, is due to some factor or determiner in a chromosome, which is called the accessory, sex, or X-chromosome, then there are three possible Mendelian interpretations. (1) Both males and females may be heterozygous—male $D(R) \times$ female $D(R)$. (2) The male may be heterozygous, $D(R)$, and the female a homozygote recessive—male $D(R) \times$ female R . (3) The female may be heterozygous, and the male a homozygote recessive—male $R \times$ female $D(R)$. This third interpretation is strongly supported by certain cases that have been carefully studied, especially the currant moth and the canary.

To suppose that the female canary is heterozygous, means that it will have equal contingents of male-producing and female-producing ova. The male bird by hypothesis will have homogeneous spermatozoa, none bearing the femaleness factor. The two contingents may be represented on this scheme :—

Ovum F	Sperm M
Ovum F	Sperm M
Ovum M	Sperm M
Ovum M	Sperm M

The chance combinations are $2FM + 2MM$; and this means equal numbers of females and males, if femaleness is dominant to maleness.

From his observations on the germ-cells of fowls

Professor M. F. Guyer has been led (1916) to regard the males as homozygous and the females as heterozygous for sex and sex-linked characters.

Physiological View.—We adhere to the view of sex expounded in "The Evolution of Sex," in 1889, that the deep constitutional difference between the male and female organism, which makes of the one a sperm-producer and of the other an egg-producer, is due to an initial difference in the balance of chemical change. The female seems to be relatively more anabolic or constructive, the male relatively more katabolic or disruptive.

A young germ-cell has, metaphorically, an alternative between two different, but equally viable, lines of life—the male and the female. It may have in its chromosome equipment an original bias in the one direction or in the other; or it may be shunted on to one line or the other by the surrounding conditions—nutritive especially. Influences which favour a preponderance of anabolic processes, which affect the nucleo-cytoplasmic relation in a manner favouring cytoplasmic assimilation, will tend to the increase of female-producing eggs. Influences that operate in the opposite direction will favour the increase of male-producing eggs.

CHAPTER X

BIRDS' EGGS

§ 1. The Making of the Egg. § 2. Yolk-forming. § 3. Maturation of the Ovum. § 4. The Male Reproductive System. § 5. Fertilisation. § 6. The Further History of the Fertilised Ovum. § 7. Early Development. § 8. Hatching. § 9. The Natural History of Birds' Eggs. § 10. Possible Uses of Egg-Coloration. § 11. Fertility and Fecundity. § 12. Sterility.

MANY reptiles lay eggs essentially like those of birds; those of tortoises and crocodiles are not very different from those of pigeons and geese respectively. Some reptiles have eggs whose shells are still flexible, and this represents a stage in the development of the bird's egg. It may be said that, as regards eggs, birds have given finishing touches to what reptiles elaborated.

§ 1. THE MAKING OF THE EGG

The history of the individual egg begins in the ovary, which has the appearance of a bunch of grapes and is attached to the wall of the body-cavity on the left side. There are to begin with two ovaries, but, for some unknown reason, the right ovary disappears and its oviduct dwindles to a vestige. As the breeding season sets in, the immature ova on the surface of the ovary begin to accumulate yolk, and many different sizes can be seen. When the egg is ripe it bursts from its encapsulating follicle and is caught up by the trumpet-shaped mouth of the oviduct. But it is necessary to look into these matters more closely.

Origin of the Gonads.—Where, it may be asked, do the reproductive organs or gonads come from? The answer in the chick seems quite clear that they arise from primitive

germ-cells which do not take any part in body-making, but are set apart at a very early date, continuing, as it were, intact the tradition of the fertilised egg-cell from which they and the body-cells arise. The old question : Does the hen make the egg, or does the egg make the hen ? was, like many similar questions, a false alternative. The fertilised egg-cell gives rise to the hen and the egg-cells thereof, or to the cock and the sperm-cells thereof. This is the general idea of the continuity of the germ-plasm which Weismann and Galton first made clear, though it had been in the minds of some of their predecessors. Galton's view was that the ovum was like a nest of organic units, to which in their entirety he applied the word *stirp*. He regarded it as directly derived from a previous nest, namely, from the ovum which gave rise to the parent. He maintained that in development the bulk of the stirp grew into the body—as every one allows—but that a certain residue was kept apart from the development of the “ body ” to form the reproductive elements of the offspring. Thus, he said, in a sense the child is as old as the parent, for when the parent is developing from the ovum a residue of that ovum is kept apart to form the germ-cells, one of which will become or may become a child. Or, as Weismann put it : “ In each development a portion of the specific germ-plasm contained in the parent egg-cell is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation.” Such in general terms is the origin of the gonads.

Is there any explanation of the suppression of the right ovary and oviduct ? Snakes show a tendency to suppress the left lung and we can interpret this as an adaptation to the narrow space of the elongated body-cavity, but why do female birds suppress the ovary and oviduct of one side, always the same side ? Perhaps for a flying creature it would be disadvantageous to have two ovaries with relatively large and heavy eggs. Perhaps it would be similarly disadvantageous to have two oviducts with relatively large and hard-shelled eggs. It may be

recalled that bats are usually uniparous. One may be reminded of the pigeon's heavy crop-full of Indian corn or grain, or of the eagle lifting the rabbit or something heavier, and it is clear that once a bird has got a-going a little additional weight is neither here nor there. On the other hand, the getting a-going is often rather strenuous and every additional ounce tells. Even the pigeon with its enormous pectoral muscles becomes terribly fatigued if it is forced to rise from the ground many times in rapid succession. It is well known that some voracious sea-birds may eat so much at a meal that they cannot fly at all for a considerable time. Therefore the reduction of weight in a flying bird cannot be dismissed as of no importance in the struggle for existence.

Perhaps there is something more important than the *weight* of an additional ovary and an additional oviducal egg, namely the reduction of the space available for the air-sacs. We admit, however, that in most birds a ventral sagittal partition divides the abdominal cavity into two distinct compartments; that the reproductive activity of birds is sharply punctuated; and that in many a bird outside of the breeding season the reproductive system has dwindled into insignificance. Yet, on general biological grounds, it is quite possible that the selection which determined the survival of females with one-sided development of the reproductive system operated during the breeding season. One must not think of each new improvement being patented separately; many siftings go on at the same time; it is the best *tout-ensemble* during the reproductive period that counts for the race.

Descending from theory to fact, we should notice that the unilateral development is not absolute. Max Kollman reports (1919) that in six cases among falcons (four of *Accipiter nisus* (sparrow hawk) one of *Astur palumbarius* (gos-hawk) and one of *Tinnunculus tinnunculus* (kestrel)) paired ovaries were found. Yet in these cases the right oviduct remained quite vestigial, which is a little puzzling. In a duck observed by Chappellier there were two ovaries

and two oviducts, and the bird sometimes laid two eggs in a day.

Origin of Germ-Cells.—There is no doubt that the primordial germ-cells of the bird are set apart from body-making cells at a very early stage in embryonic development. In the chick, according to Charles H. Swift (1914), the primordial germ-cells appear between the endoderm and the ectoderm in a crescent at the margin of the area pellucida, anterior and antero-lateral to the embryo. They are seen during the primitive streak stage, while the embryo has only about three segments. Subsequently by amœboid movements they enter the mesoderm and the incipient blood-vessels of the mesoderm. They are carried at first by their own movements, and later by that of the blood, to all parts of the embryo and vascular area. They remain generally distributed in this way until the embryo has about twenty segments or somites. They seem to concentrate in the direction of the future reproductive organ, but this may be in part more apparent than real, for they degenerate elsewhere.

The important general fact is that the primordial germ-cells or sex-cells appear very early in the development of the body of the embryo. According to Swift (1915) the germinal epithelium which forms the foundation of the reproductive organs is well-defined between the 80th and 90th hours of incubation in the fowl. There are recognisable primordial sex-cells in this germinal epithelium, and, as we have mentioned, there are others outside its limits, some of which at least are known to undergo degeneration.

Multiplication or proliferation of cells occurs in the germinal epithelium, and the result is the formation of "sex-cords." These sex-cords of the first proliferation are epithelial in character, and the primordial sex-cells, which are present in them, do not seem to have anything to do with their formation. But it is possible that some of the germ-cells stimulate the epithelial cells around them to activity. The cords of first proliferation become seminiferous tubules in the testes, medullary cords in the ovary. When

they are formed, about the seventh day, it is possible to distinguish the sexes, for the number of primordial sex-cells remaining in the germinal epithelium after the formation of the cords of first proliferation is small in the male, and not greatly diminished in the female.

The strands of first proliferation are ephemeral as in mammals. They disappear a few days after hatching, and a chicken a fortnight old shows not a trace of them. Their place is taken by a second proliferation of germinal epithelium—the cortical strands—which form the cortical zone of the ovary, and it is from their elements that the definitive ova arise. Firket (1914) points out an interesting contrast between the medullary strands and the cortical strands of the ovary. The former illustrate retrogressive changes, for the immature ova they produce, though numerous at the end of incubation, never come to anything, and never get a follicular envelope. The cortical strands, on the other hand, show progressive changes; they form the ova which become invested in a follicular envelope.

Beginning with the 8th day, but especially during the 9th, 10th, and 11th days of development, there is a rapid increase in the number of primordial sex-cells or oogonia in the germinal epithelium of the female embryo. They form groups, which are the results of successive divisions, and give rise to lobulations or buds on the deep surface of the germinal epithelium. These buds are composed chiefly of oogonia, but they include cells of peritoneal origin. As the buds increase in size and become the cortical cords or the cords of second proliferation, the oogonia become definitive ova, while the peritoneal cells of the germinal epithelium, present in the cords, develop the follicular epithelium, which forms an envelope round the growing egg.

Looking backwards we may distinguish in this complicated history the following stages in the development of the bird's ovary:—

(1) Primordial sex-cells (“primary gonocytes”) appear very early, and do not share in body-making. They migrate in the embryonic tissue, and most of them probably

degenerate. But some of them reach a definite locus—the germinative epithelium.

(2) A special portion of mesoderm gives rise to the “uro-genital connections,” the “rete ovarii” in the case of the ovary. Of similar origin is the connective-tissue framework.

(3) The germinative epithelium gives rise by proliferation to buds or strands, the first set transient, the second set including the secondary gonocytes.

Two points of general biological interest must be noticed.

(a) The appearance of primordial sex-cells on the second day of embryonic development illustrates the early segregation of reproductive cells, and is in perfect harmony with Weismann's doctrine of the continuity of the germ-plasm. Yet the connection between these primordial sex-cells and the secondary gonocytes which form the definitive eggs and sperms is not very clear. It may be, as Firket suggests, that the primordial sex-cells have only a historical interest, that they are the vestiges of an old-fashioned method of gonocyte-production which persists in Cyclostomes and Lancelets. (b) Among the possible ova produced from the secondary gonocytes in the cortical strands of the ovary there is a sort of struggle for existence, and only a small percentage attain to maturity. If there is any discriminateness in the intra-ovarian elimination that goes on, it may be of some importance in evolution—securing the survival of certain types of ovum-constitution.

§ 2. YOLK-FORMING

The young egg-cells or oocytes in the ovary accumulate nutritive reserves of yolk, which is brought to them by the blood and the lymph in the form of dissolved proteins and fatty acids. Acting on this material, the immature egg-cell lays it down within itself in the form of minute “yolk plates.” The increase in the size of the immature egg comes about very rapidly in birds, as also in reptiles. Riddle (1916) notes that when the oocyte or young ovum of the fowl reaches a diameter of 6 mm. the ratio of growth suddenly (within a

day) increases twenty-five fold—mainly by the rapid addition of yolk.

There is a central core of what is called "white yolk" (really yellow), physically different from the "yellow yolk," and there are zones of "white yolk" occurring at intervals amongst the "yellow yolk." The difference between the "white yolk" and the "yellow yolk" depends on the nature of the minute "yolk-plates," which are laid down in

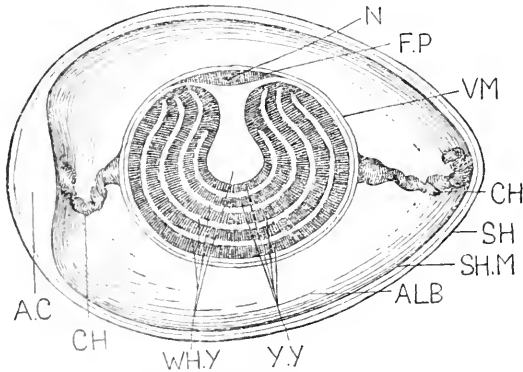


FIG. 38.—Diagrammatic section of egg. N., nucleus; F.P., formative protoplasm; V.M., vitelline membrane; C.H., chalaza; S.H., shell; S.H.M., shell-membrane; A.L.B., albumen; Y.Y., yellow yolk; W.H.Y., white yolk; A.C., air-chamber.

concentric layers, and the white yolk has more water in it than the yellow yolk. It is a familiar fact that the yolk of a hard-boiled egg shows alternating zones. On the top of the central core of "white yolk" there is a clear drop of living matter centred in a nucleus. This is the formative protoplasm of the ovum, out of which an embryo may be developed. However the laid egg be turned about, the dilated egg-cell (popularly called the yolk) turns so that the formative disc is uppermost, and this is important because the movement brings it nearest the brooding mother, the source of warmth.

Part of the yolk of the egg is of a fatty nature, and it is interesting to notice that there is a correlation between the fat content in the blood of fowls and the total egg records. The correlation is positive for birds in a laying condition;

it sinks to zero after the cessation of laying ; and it finally takes a high negative value in birds which have long ceased to lay (Riddle and Harris, 1918).

But part of the yolk of the egg is of a protein nature, and the size of the egg—affected by the amount of albumen as well as by the amount of yolk—is probably influenced by changes in the protein-metabolism of the hen bird. Giving ring-doves (*Streptopelia*) small doses of quinine-sulphate reduces the yolk size and the total size of the eggs, and it is known that quinine reduces the destruction of the nitrogenous components of the tissues, and would therefore probably check the formation of albumen by the walls of the oviduct and also the characteristic transformations of nitrogenous compounds in the egg itself (Riddle and Anderson, 1918).

The yolk consists of

phosphatides	20·6	per cent.
neutral fats (chiefly lecithin)	49·5	„ „
protein (chiefly vitellin)	28·4	„ „
				<hr/>	
				98·5	

the residue being mineral matter and water.

Egg-Envelopes.—The term vitelline membrane is properly applied to the delicate non-cellular layer immediately around the yolk-containing ovum. It is the cell-wall, and is clearly seen in the young ovarian ovum. But matters do not long remain so simple. As Lécaillon (1910) has shown, there is outside the non-cellular vitelline membrane a median layer of degenerating epithelium, and outside that again an external layer of fibrillar connective tissue. The two layers outside the true vitelline membrane are contributed by cells of the ovarian follicle. The whole envelope would be better called the vitelline capsule. Its complexity is an adaptation to the large amount of yolk which makes the ovum a much bloated cell. The firmer capsule prevents bursting when the egg is liberated from the ovary and begins to pass down the oviduct.

Dwarf Eggs.—It is not very uncommon for a hen to produce dwarf eggs, sometimes spheroidal, occasionally cylindrical. They have been studied by Raymond Pearl and Maynie R. Curtis (1916), who find that 35 per cent. are yolkless. In those which contained yolk, 9 per cent. had no enclosing membrane. The production of a dwarf egg is usually an isolated phenomenon, occurring during the height of the breeding season, and not implying that there is much wrong. In eleven out of two hundred cases, however, no normal eggs were produced after the dwarf egg, and examination showed, in five of these, some pathological condition of the oviduct which interfered with the passage of the egg. A dwarf egg means in most cases that the egg has not received its proper equipment of yolk, perhaps through being liberated from the ovary prematurely. In most of the other cases it means that a shell has formed in the oviduct around a blob of albumen.

Double-Yolked Eggs.—When two ova are liberated from the ovary within an unusually short interval of one another, they are apt to unite in the oviduct. According to the level in the oviduct at which they come together, different types arise. These have been studied in the fowl by Maynie R. Curtis (1915), who distinguishes three types, connected by gradations. In one type (16.03 per cent.) the two yolks (or ova) share the same ensheathments within the shell; in a second type (70.99 per cent.) the layers that form the chalazæ are separate for the two, but all or part of the thick white of egg is common to the two; in a third type (12.98 per cent.) the two yolks have entirely separate thick albumen envelopes, but are within a common shell-membrane. It is noted that the occurrence of double-yolked eggs may indicate a heightened fecundity, but it may also indicate a low physiological tone in the oviduct.

Triple-yolked eggs are very rare. Maynie R. Curtis (1914) notes that in the course of six years only three triple-yolked eggs were obtained from more than three thousand fowls. Each was the first egg of a young pullet, as is often the case with double-yolked eggs. An egg

with three yolks represents the extreme of rapid egg-production ; it is in line with the production of two eggs united by a membranous tube, or of two eggs simultaneously, or of two eggs on the same day. The yolks or the yolk-laden ova come together in the oviduct and are enclosed in one shell ; the particular type depends on the position in the oviduct, between the funnel and the isthmus, where the coalescence takes place.

An interesting correlation exists between an increase in the comb in hens and the incidence of an egg-laying period. Geoffrey Smith showed (1911) that the increase of the comb in the hen is due to a fatty infiltration of the central connective tissue core of the comb, and that decrease is due to the abstraction of fat. The cock's comb contains only comparatively small quantities of fat in the central core, the substance of the comb consisting mainly of fibrous connective tissue. The cock's comb does not exhibit marked fluctuations in size as the hen's does. Geoffrey Smith pointed out further that the increase in the hen's comb is not accompanied by a rise in general body-weight, though such a rise usually occurs some time *before* the enlargement. The explanation of the fatty infiltration is to be found in the fact that at the egg-laying periods the blood becomes charged with fatty material which is conveyed to the ovary and forms part of the yolk of the ova. The excess of this fatty material is deposited in the comb, and probably in other situations as well.

A little point of some interest in connection with egg-laying in hens is that the yellow pigmentation about the head and legs seems to decrease in the course of vigorous egg-laying. It is suggested by A. F. Blakeslee and D. E. Warner (1915) that the laying removes yellow pigment in the yolks more rapidly than it can be replaced by the normal metabolism, and that in consequence the ear-lobes, the beak, and the legs become pale by the subtraction of pigment. It is not against this suggested correlation to point out that other conditions apart from egg-laying may bring about a similar paleness.

§ 3. MATURATION OF THE OVUM

In the middle of the drop of formative protoplasm on the top of the yolk lies the relatively large nucleus, containing readily stainable nuclear rods or chromosomes, definite in number for each species. These are the vehicles of parts at least of the hereditary equipment.

At a certain stage, while still in the ovary, the egg-cell undergoes a remarkable process called maturation. The nucleus shows signs of activity; its membrane disappears, admitting of a freer give-and-take between the nucleoplasm and the general cytoplasm of the cell; and it divides twice in rapid succession, forming two polar bodies—minute sister cells of the ovum that come to nothing. One result of this maturation is that the number of chromosomes in the nucleus is reduced to one half of the normal number, probably in the formation of the first polar body. This is called a “reducing division” or “meiotic division,” and it is very different from the ordinary cell-division that goes on continually in developing and growing structures.

If we compare a nucleus with its chromosomes to a box of wooden matches we may think of two possible ways of halving these with precision. Half of the matches may be taken out and put into a separate box—this would correspond to reducing division. Or each match might be split into two longitudinally, so that the number of useable matches remains the same, the two sets of split halves being put in separate boxes. This is what takes place in ordinary or equation division. As a similar reduction takes place in the history of the male's germ-cells or spermatozoa, it is plain that in fertilisation the normal number will be restored,

$\frac{n}{2} + \frac{n}{2} = n$. So it is evident that the maturation divisions of the egg-cell mean, in part, a preparation for fertilisation. To this it is now necessary to turn.

§ 4. THE MALE REPRODUCTIVE SYSTEM

The essential male-organs or testes, which make the spermatozoa, arise, like the ovary of the female, as patches of germ-cells on the wall of the body-cavity of the embryo.

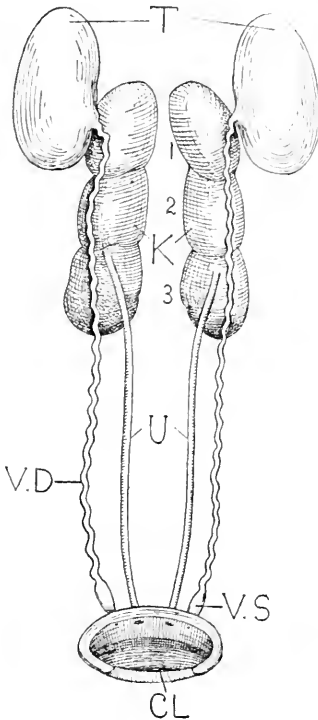


FIG. 39.—Male reproductive organs of cock. From a specimen. T., testes; K., kidneys; 1, 2, 3, lobes; U., ureters from kidneys; v.d., vas deferens from testis; v.s., seminal vesicle, a slight dilatation for storing sperms; CL., cloaca.

Within the testes there is a multitudinous multiplication of germ-cells, spermatogonia dividing into spermatocytes, and these into more spermatocytes, the final generation of these differentiating into the fertilising cells or spermatozoa. In the course of the spermatocytic division there is a reducing division, comparable to that in the maturation of the ovum, so that the ripe spermatozoa

have $\frac{n}{2}$ chromosomes.

The spermatozoa pass from the testes by fine ducts (vasa efferentia) into a convoluted body (the epididymis), and thence into the main duct or vas deferens which leads into the cloaca. The ends of the two vasa deferentia are often dilated to form seminal vesicles—store-chambers for spermatozoa; and the whole length of the vas deferens is characteristically convoluted or zig-zagged from side to side when it is full of sperms.

In most cases the spermatozoa are transferred from the cloaca of the male to the cloaca of the female in the sexual union or "treading." Only in a few cases is the trans-

ference facilitated by the development of a grooved muscular organ or penis, which has its antecedent in Crocodilian and Chelonian reptiles.

This is not continuous with the male ducts as it is in mammals, but rises from the wall of the cloaca. It is practically confined to the Ratitæ and to duck-like birds, but a rudimentary one occurs in a few Carinatae. It is well-developed in the Great Tinamou and rudimentary in *Crypturus*, both members of the family of Tinamous which many authorities would refer to the Ratitæ. Gerhardt (1908) has described a well-developed penis in the Crested Curassow, *Crax alector*, and Tschudi reports the same for the Guan, *Penelope abourri*, which belongs to the same Gallinaceous family of Cracidae.

It is of some interest to find that there is sometimes asymmetry in the testes as well as in the ovaries. Raymond Pearl (1908) notes that in adult doves and pigeons, if quite healthy, the right testis is larger than the left in a very high percentage of cases. The left testis, in a high percentage of cases, is absolutely longer and thinner than the right, more nearly approaching the shape of the persistent (left) ovary. In disease—particularly in tuberculosis—the testes undergo extreme atrophy (often 90 to 95 per cent.); the reduction is greater in the right testis than in the left. In hybrids the normal size relations of the two testes are much disturbed.

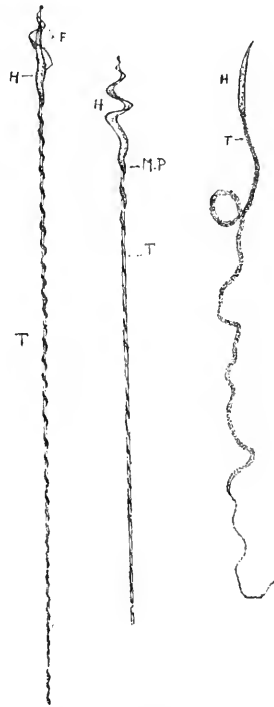


FIG. 40.—Three forms of spermatozoa in birds. H., the head, containing the chromosomes; T., the tail, which is locomotor in function; M.P., a middle piece in which there lies a minute centrosome; F., a delicate fringe on the head. It must be noted that a hundred spermatozoa can swim about in a drop of fluid suspended from the head of a pin; they are extremely minute cells.

The spermatozoa of birds are typical, showing (*a*) a "head" mostly consisting of the chromosomes, which are certainly the vehicles of at least a great part of the hereditary qualities (for there is a minimum of extra-nuclear cytoplasm) (*b*) a minute "middle piece" bearing a "centrosome," which afterwards plays an important part in the division of the fertilised egg-cell; and (*c*) a locomotor "tail" which is left outside when the spermatozoon enters the ovum.

It is in the nature of typical spermatozoa, little more can be said, to move against a current. This can be demonstrated experimentally under the microscope. Now as there is a slight downward current of secretion in the oviduct of the female bird, the spermatozoa will tend to meet the ova. This meeting may be at the top of the oviduct. In some cases the meeting is believed to be in the ovary itself. What does the fertilisation imply?

§ 5. FERTILISATION

Fertilisation may be defined as the intimate orderly union of two sex-cells, the spermatozoon and the ovum. It is a microscopic business; the transference of spermatozoa from the male to the female should be designated by a different term—insemination.

(*a*) Fertilisation implies the mingling of two inheritances, or of the "factors" of two inheritances, the paternal and the maternal. These "factors" or "genes" or determinants of hereditary qualities are carried in great part by the chromosomes, which are equal in number in ripe ovum and ripe spermatozoon. It may be, however, that some of them are carried in the extra-nuclear cytoplasm or cell-substance of the germ-cell. Whether this be so or not, it is certain that the extra-nuclear cytoplasm is very important in furnishing initial building material. But as the amount of cell-substance or cytoplasm, as distinguished from chromosomes or nucleoplasm, is infinitely minute in the spermatozoon compared with the amount in the ovum (the formative droplet already alluded to), it seems impossible to avoid the conclusion that

the mother must in this respect count for more than the father. The ovum furnishes more of the initial building material—"the organ-forming substances." When there is, as in mammals, a close ante-natal partnership between mother and offspring, there is another way in which the mother counts for more than the father. But there is nothing of this sort among birds, except in so far as it is the mother that furnishes all the legacy of yolk on which the developing embryo depends until it is hatched.

(b) Fertilisation implies a restoration of the number of chromosomes to the normal ($\frac{n}{2} + \frac{n}{2} = n$), and in the fact that each parent furnishes only half the normal number of chromosomes, there is a hint of the important conclusion that the male and female parents contribute different items—more subtly than is suggested by warp and woof—to the web that will be woven, namely, the young creature.

(c) The spermatozoon introduces into the egg-cell a minute body called the centrosome, which plays an important part in the segmentation or cleavage that is shortly to follow. This centrosome divides into two and these take up their positions at opposite poles of the conjoint nucleus and give origin to delicate plasmic radiations which have something to do with the division of the chromosomes to form two daughter-nuclei in the first segmentation or cleavage. In every subsequent cell-division, all through development and after, two centrosomes play the part of "the weavers at the loom." They are centres of great protoplasmic activity.

(d) Whenever a spermatozoon has entered an ovum, a rapid change occurs in the periphery, which is partly of the nature of an oxidation. The result is a "blocking" of the egg to the entrance of other spermatozoa. The egg-cell becomes, as it is said, "non-receptive." Although there are cases where several spermatozoa enter an egg-cell at once without doing apparent harm, there are other cases known where "polyspermy," as it is called, leads to monstrosities by setting up several non-unified centres of cleavage.

Probably, therefore, it is advantageous that the egg-cell should rapidly become non-receptive when one spermatozoon has entered.

(e) But fertilisation must imply something more, for it is followed by segmentation or cleavage, which does not usually occur in the absence of a fertilising spermatozoon. Whether it is that the spermatozoon introduces some positive stimulus, such as a ferment, activating the nucleus of the egg so that division sets in ; or whether it is that the entrance of the spermatozoon removes or counteracts some inhibiting influence which was keeping the ovum from beginning to divide ; it would be rash at present to say. It may be noted that the researches of Delage, Loeb, and others have shown that it is possible in a variety of ways to induce aspermic (or artificially parthenogenetic) development in eggs, but this has not yet succeeded above the level of frogs.

There have been various reports of futile attempts at parthenogenetic development in the eggs of fowls. Thus A. Lécaillon (1909) observed in unfertilised eggs of the fowl the formation of a disc of cells, taking place by slow division of the usual (mitotic) type. The appearance of the cells was abnormal, and all of them underwent degeneration.

Artificial insemination of hens and pheasants has been effected (E. Ivanow, 1913), and a small percentage of the hens laid fertile eggs which developed.

§ 6. THE FURTHER HISTORY OF THE FERTILISED OVUM

When the ovum is liberated from the ovary it is caught by the adjacent trumpet-shaped mouth of the oviduct. Fertilised either at the top of the oviduct or previously, it begins to pass slowly downwards, developing as it does so, and undergoing a succession of interesting changes. It is surrounded by various instalments of white-of-egg or albumen ; it is surrounded by a shell-membrane and a calcareous shell ; the shell is usually stained with pigments before it is finally set ; it is moved onwards, broad end foremost, and is finally expelled through the cloaca by the

muscular action of the lower part of the oviduct. But it is instructive to consider these events more precisely.

The liberation of an ovum from the ovary is due to the rupturing of the follicle, and that is probably due to the increased internal pressure incident on the continued accumulation of yolk in the egg.

It is normal for the funnel-shaped end of the oviduct to be pressed against the ovary, so that it embraces the ripe follicle and receives the liberated ovum. But it has been proved by Raymond Pearl and Maynie R. Curtis (1914) that the pressure from the funnel is not necessary for ovulation.

The same investigators point out that various things may happen when ova are not caught by the funnel of the oviduct but go astray into the body-cavity. First, they may cause serious and fatal disturbances; second, they may be absorbed rapidly from the general peritoneal surface; or third, they may be walled off by the peritoneum and then absorbed. If the first of these things happens, it means that the bird is not in a very vigorous condition, for absorption is usually facile, and it does not seem to be unprofitable.

The abdominal viscera are so disposed that they form a sort of pocket in which the ovary lies, and Maynie R. Curtis

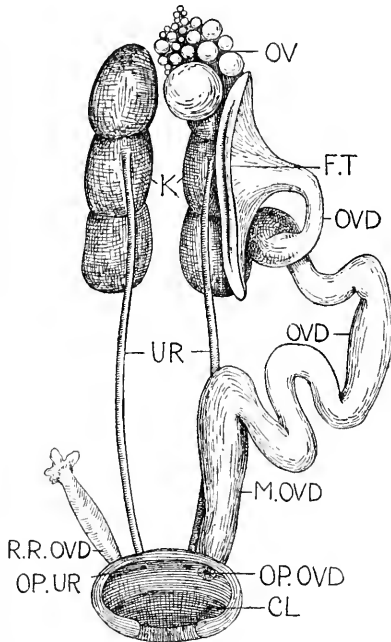


FIG. 41.—Female reproductive organs of a hen. From a specimen. ov., the ovary; K., the kidneys; F.T., funnel that grips the egg; OVD., oviduct; M.OVD., muscular part of oviduct; OP.OVD., opening of oviduct; UR., ureters from the kidneys; OP.UR., opening of right ureter; R.R.OVD., rudimentary right oviduct; CL., cloaca.

has shown (1910) that this walling off of the ovary tends to direct liberated ova into the mouth of the oviduct. Apart from the musculature in the wall of the oviduct, some importance in moving the egg downwards is also to be attached to the dorsal and ventral bands, partly muscular and partly ligamentar, which run from the oviduct to the wall of the body-cavity.

The best description of the bird's oviduct is that given by F. M. Surface (1912) in reference to the hen. As the matter is very important in connection with the equipment of the egg, some details must be given.

The internal surface of the oviduct is thrown into a number of primary longitudinal ridges, over which the epithelium forms secondary folds. In the region badly called the uterus, the ridges as such are lost, but their place is taken by a number of leaf-like folds.

The first region is that of the *funnel* which grips the ovum liberated from the ovary by the bursting of a follicle. Anteriorly it shows "glandular grooves," accumulations of gland-cells at the bottom of the grooves between the secondary folds of the epithelium. Further back it shows unicellular glands among the ciliated cells. These unicellular glands occur in all parts of the oviduct except the anterior portion of the funnel. The funnel glands perhaps secrete the chalaziferous layer—a very thin layer of dense albuminous substance next the yolk.

The second region is the coiled *albumen region*, with a thick layer of "tubular glands," consisting of long convoluted and branched tubules, opening into the lumen of the oviduct by short epithelial ducts and secreting large quantities of albumen. They are homologous with the glandular grooves of the anterior portion of the funnel, and they occur in all parts of the oviduct between the funnel and the vagina. There are also, as already indicated, unicellular glands among the ciliated cells. These two sets of glands form the dense albumen outside the chalaziferous zone.

The third region is known as the *isthmus*; it is separated off from the albumen region by a line without tubular

glands. In the isthmus itself there are tubular glands and unicellular glands as in the albumen region. The isthmus forms the shell-membrane, but also some albumen.

The fourth region is called the *uterus*, in which there are tubular and unicellular glands, but the former have a somewhat different appearance from those in the isthmus and the albumen region. As Pearl and Curtis have shown, the uterus not only forms the shell, but secretes thin albumen which must pass through the shell and the shell-membrane by osmosis.

The fifth region is the *vagina*, from which tubular glands are entirely absent, but the usual unicellular glands occur. In the vagina these glands are perhaps concerned in secreting the delicate outer shell-cuticle and the pigment. In other parts of the oviduct the unicellular glands are probably concerned for the most part in making a fluid or thin albumen.

Pearl and Surface (1909) have made it clear that the stimulus which excites the shell-secreting glands of the oviduct (in the fowl at least) is mechanical rather than chemical in nature. Moreover, the formation of the shell is brought about by a strictly local reflex, and is not immediately dependent upon the activity of other portions of the reproductive system.

A cross-section through the wall of the oviduct shows, from the outside inwards, the following layers :—

- (1) A peritoneal investment,
- (2) A longitudinal muscular layer,
- (3) Connective tissue with blood-vessels,

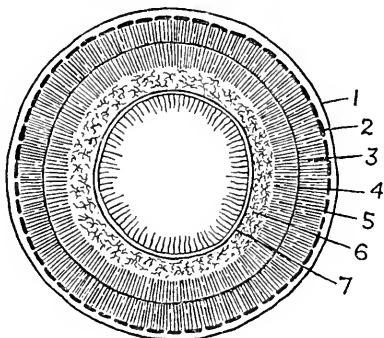


FIG. 42.—Diagrammatic cross-section through the oviduct of a bird. 1, peritoneal investment; 2, longitudinal muscular layer; 3, connective tissue and blood-vessels; 4, circular muscular layer; 5, another layer of connective tissue; 6, glandular layer; 7, internal ciliated epithelium with unicellular glands.

- (4) A circular muscular layer,
- (5) More connective tissue,
- (6) A thick layer of branched tubular glands except in the funnel and the vagina, and
- (7) An internal lining of ciliated epithelium, with unicellular glands except in the anterior part of the funnel.

Ovum in Ovo.—An egg within an egg is not very uncommon in the case of fowls. According to Parker, doubleness in eggs is due to an abnormal ovary, or to an abnormal oviduct, or to both combined. Two ovarian follicles may combine, or two ova may be liberated simultaneously, but both these phenomena are rare. More frequently two ova may be liberated from the ovary with an abnormally short interval between them. If two ova are in the oviduct at the same time a disturbed rhythm of contraction (“antiperistalsis”) may press a small enshelled egg up against an egg not yet enshelled, and the two may be surrounded by a second shell. Or it may be that a false egg, *i.e.* a mass of albumen surrounded by a shell, may be pressed into close contact with a normal egg not yet covered with a shell, and the two may be covered by a second shell.

Twinning.—Twin-embryos within one egg-shell are of occasional occurrence in birds, but they are not always of the same nature. According to E. S. Ruth (1916), three types may be distinguished in ducks. (*a*) Dissimilar twins within one egg-shell imply two or more fertilised ova within one shell, or possibly a multinucleate ovum. (*b*) Identical twins within one egg-shell result from the early separation of parts of the segmenting embryonic area. (*c*) Belonging to the same category are joined twins or duplicities, probably due to a separation of parts of the segmenting embryonic area (the blastoderm), but an incomplete separation.

§ 7. EARLY DEVELOPMENT

In appropriate conditions of temperature, usually afforded by the brooding bird, the fertilised egg proceeds to develop.

The minimum temperature for a hen's egg is 28° C. The drop of formative protoplasm on the top of the yolk divides and redivides and forms a disc of cells—the blastoderm. This soon proceeds to spread over the yolk, but the essential events take place in an oval area in the middle of the upper surface. Even on the first day the nervous system begins to develop, appearing as a median longitudinal groove; and soon the foundations are laid of food-canal, musculature,

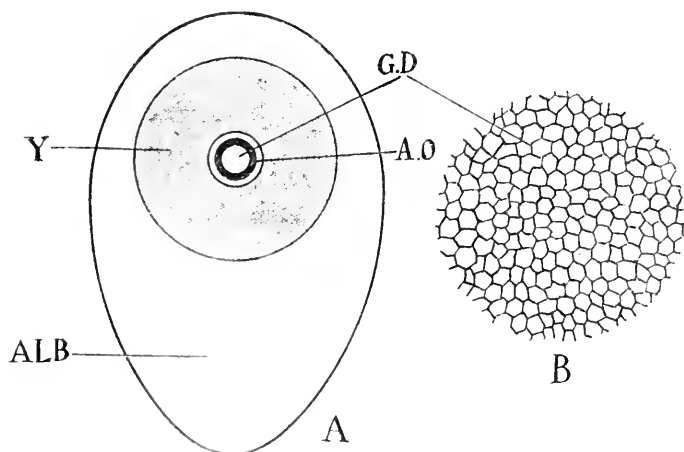


FIG. 43.—A, The embryonic disc seen from above. Suspended in the white of egg (ALB.) is the ovum proper, the egg-cell dilated with yolk (Y.). A formative drop of protoplasm divides and redivides, so that a disc of cells results (G.D.). The central part of this disc or blastoderm is thin and translucent (the area pellucida); the marginal part is thicker and less transparent (the area opaca (A.O.)). At the inner rim of the area opaca, bordering the area pellucida, there is an abundant development of blood-vessels—the area vasculosa. B, Much enlarged view of embryonic disc or blastoderm, seen from above, showing a pavement-like area of cells.

skeleton, and the like. Very rapidly, though often intermittently, the development goes on—one of the most familiar and one of the least intelligible processes in the world.

Out of apparent simplicity—a drop of living matter on the top of the yolk—there emerges obvious complexity. We know what is taking place—the various items or factors

in the inheritance are finding expression, are being actualised ; but we do not understand the process. Development is the making visible of the latent manifoldness of the inheritance. It always implies two things—differentiation and integration. Differentiation is the structural side of division of labour—the appearance of nervous, muscular, glandular, skeletal, and other cells. Integration means regulating and harmonising the whole creature, binding its parts together into a well-controlled unity.

Development implies a multiplication of cells, an arrangement of these in various ways, and then the establishment of the differences between them—some becoming nervous, some muscular, some glandular, some skeletal, and so on.

The multiplication of cells is usually effected by the familiar but mysterious process of cell-division, in the course of which each of the nuclear bodies or chromosomes (occurring in definite number in each species) is split lengthwise, so that each of the two daughter-cells gets a meticulously exact half of the nuclear equipment of the parent-cell.

In parts of chick-embryos cultivated in nutritive solutions the process of cell-division has been carefully *timed* by Warren H. Lewis and Margaret R. Lewis (1917). A common period was between two or three hours for the complete process, but some cells went through the whole intricate process within one hour.

The succession of steps in the development is very well known, especially in a familiar type like the chick, but the actual “go” or physiology of the development is very obscure. We sympathise with Harvey’s words on “the efficient cause of the chicken” :—

“Although it be a known thing subscribed by all, that the fœtus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the school of physicians nor Aristotle’s discerning brain have disclosed the manner how the cock and his seed doth mint and coine the chicken out of the egge.”

At a very early stage the developing embryo of the bird

begins to be "folded off" from the yolk. As a result of this the embryo is attached by a relatively narrow stalk to the large yolk-sac, over which the extra-embryonic blastoderm spreads, showing blood-vessels before the end of the first day. The yolk is gradually utilised and, just before hatching, the greatly reduced sac is withdrawn into the body-cavity of the embryo and the navel or umbilical opening closes up.

Of great importance are the two embryonic membranes—the *amnion* which forms a protective hood over the embryo,

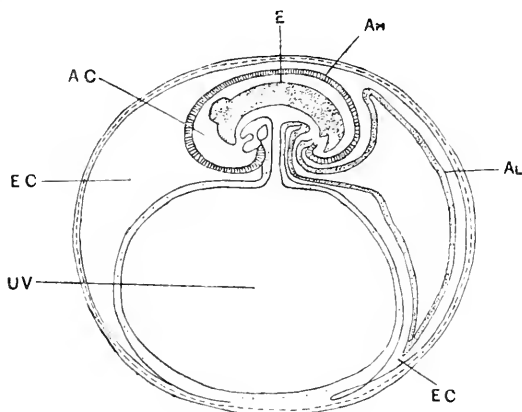


FIG. 44.—Diagram of developing embryo of bird (after Grosser). Showing the embryo (E.); the inner or true amnion, a protective hood (AM.); the amniotic cavity containing fluid (A.C.); the extra-embryonic body-cavity (E.C.); the allantois (AL.); the external serosa includes the outer amnion and the vitelline capsule; the yolk-sac (U.V.) full of yolk.

and the *allantois* which spreads as a delicate hood underneath the shell. Blood-vessels from the embryo are distributed abundantly on the allantois, and serve to capture the oxygen which diffuses through the shell from the outer world. Carbon dioxide diffuses out. If the shell be varnished, so that its pores are closed, the embryo must die. The allantois is thus the embryo's breathing organ; but as it also absorbs some white of egg and receives nitrogenous waste-products from the embryo, it may also be reckoned as a nutritive

and excretory organ. This is interesting in connection with the fact that in ordinary mammals the allantois combines with part of the amnion to form the placenta—an intricate structure that binds the unborn mammal into partnership with its mother. Now the placenta enables the embryo mammal to capture oxygen from the maternal blood and to get rid of CO_2 ; it also serves for the capture of fluid food

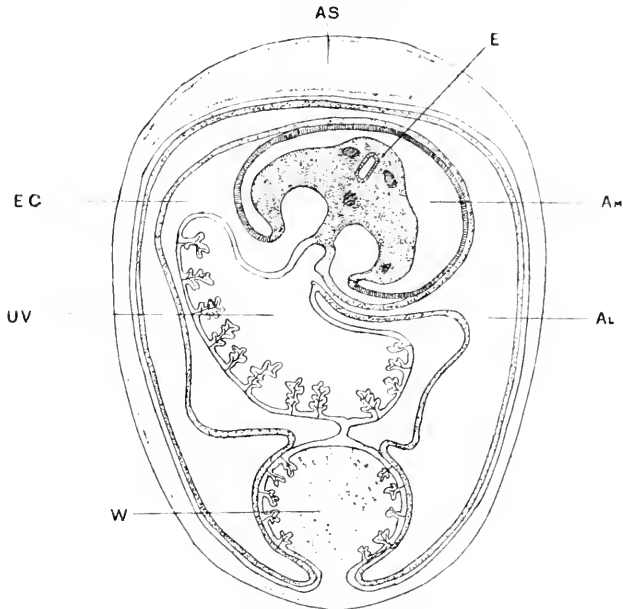


FIG. 45.—Diagrammatic vertical section of bird embryo (after Grosser). Showing the embryo (E.); the amniotic cavity (AM.); the allantoic cavity (AL.); the yolk-sac (UV.); the albumen (W.); the extra-embryonic body cavity (EC.); the serous membrane (AS.).

from the same source and to get rid of nitrogenous waste. In other words, it functions like the allantois of birds.

Eventually the young bird, often provided with an "egg-tooth" (a hardening of horn and lime at the tip of the upper jaw), perforates the membrane of the air-chamber at the broad end of the egg, and gets its first breath. The air fills the hitherto functionless, but steadily developing, lungs. Important changes take place very rapidly in the circulation;

the navel closes up ; the allantois shrivels ; and the young bird breaks open the doors of its prison.

Development implies a realising or actualising of what is implicit or potential in the inheritance. It means a cashing of the legacy. This is not possible unless certain conditions be fulfilled—a certain amount of oxygen, a certain degree of warmth and humidity. The conditions of development form the normal “nurture,” and peculiarities in the nurture will influence the expression of the inheritance. Thus Miss Florence M. Alsop has shown (1919) that the development of the nervous system of the chick is affected by changes of temperature. It is quickened by raised temperature and retarded by lowered temperature, while excessive temperatures on the plus side induce a large percentage of abnormalities, either in the brain or in the spinal cord.

It is not very unusual to find chick embryos showing abnormalities. One of the commonest is some form of duplicity. Sometimes this occurs near the beginning, for the blastoderm (or disc of embryonic cells) may show four primitive streaks instead of the normal one. Sometimes there is an almost complete duplication of structures on one blastoderm. Sometimes there may be a common head-region and a duplicated embryonic body, and it is very difficult to draw the line between this and cases where the living chick has an extra pair of hind legs. It may seem far-fetched to regard an extra pair of hind legs as comparable to a twin, but the gradations are many. In several cases we have seen that the presence of an extra pair of hind-legs is associated with the presence of an extra cæcum at the junction of the small intestine with the large, enough of itself to show that the duplication is more than superficial. There are cases, however, where a duplication of a limb is of a different order, being due to some pressure on the primordium of the limb, which involved a splitting into two independently developing parts.

We speak of the *vita minima* of the embryo and that is indeed true ; it is often a flickering flame which a gust may blow out altogether. On the other hand, there is often a

remarkable vitality in the embryo, and this is well illustrated by the ready way in which wounds of a chick's blastoderm are healed. The process can be watched for hours in hanging-drop preparations. In wounds of the extra-embryonic part of the blastoderm all the three germinal layers take part in the process, but the ectoderm and the endoderm are somewhat more active than the mesoderm. There is de-differentiation or simplifying; then fusion of cells as if they were helping one another; then re-differentiation or re-establishment of the old complexity. Wounds in the embryo itself are mainly healed by the ectoderm cells. There is de-differentiation of the ectoderm and amœboid migration of the ectoderm cells over the wound. The mending is just like a special case of the regenerative capacity which developing structures possess in a high degree (Poynter, 1919).

The inheritance of an organism consists of a large number of initiatives or "factors" which develop when the appropriate liberating stimuli are present. They express themselves as the gramophone record does when the spring is released. The initiatives or factors are germinal differentiations representative of the organism's characters, and some of them have what one might call a strong inertia. If the minimal vital conditions are present, the potentialities unfold. Thus up to a certain point the complex structure of the bird's lung is established although the lung is not in use. Beyond a certain point, however, the lung will not develop unless the young bird breathes actively in the open air. And this is important, for the fullness of development depends in most cases on some measure of activity. It is not a passive unfolding, it is an active trading with time and circumstance. A fully developed character is always a *product* of the inherited "nature" and the appropriate "nurture," which includes use and exercise, as well as food and suitable surroundings.

Another biological idea that must be kept in mind in thinking of development is the general tendency to recapitulate stages in racial evolution. In the differentiation

of organs, such as brain, heart, kidneys, there is a re-treading of the old historical path. Thus the kidneys, which are eventually organs of some compactness, begin as a double row of kidney-tubes, taking our thoughts back to worms. Or, again, every embryo bird has a transitory notochord—the permanent skeletal axis in pioneer Vertebrates like lancelets and lampreys. And every embryo bird has its gill-slits. There are abundant illustrations of the lien that the past has on the present. The fact is that the past lives on in the present, and ontogeny (or individual development) tends in a general way to recapitulate phylogeny (or the evolution of the race). Yet this idea of *recapitulation* must be held in the mind along with the idea of *specificity*; for after a few days have passed the embryo bird is on an avian path, and the duck embryo is different from the fowl-embryo.

§ 8. HATCHING

When the young chick within the egg is about twenty-one days old, it thrusts its beak into the air-chamber at the broad end of the egg. Air enters the nostrils and fills the lungs for the first time, and in the exhilaration of this first breath the unhatched chick knocks the “egg-tooth” at the tip of its beak against the inside of the shell and breaks a way out.

Professor Franz Keibel has inquired into the musculature involved in breaking the shell. He finds that the work is done by a special muscle—the *musculus complexus*—which is temporarily exaggerated in strength and is used to jerk the beak upwards and backwards against the shell. And just as the egg-tooth—an instrument which only functions once—falls off soon after hatching, so the *musculus complexus*, having done its work, becomes in a few days relatively smaller.

Keibel's account of the hatching of the chick is not borne out by A. G. Pohlman's re-investigation (1919). The *musculus complexus* does attain a maximum size before and

at the time of hatching, and it does show a progressive atrophy after the chick is hatched, to the eighth day at least. But the state of the muscle is peculiar before the time of hatching. It is infiltrated with lymph and this is associated with the complete incorporation of the yolk-sac and with the discharge of blood from the vessels of the allantois, whose function is over, into the systemic vessels of the chick. The infiltrated *musculus complexus* is physiologically incapacitated from pronounced muscular contraction, so that it cannot be instrumental in breaking open the prison doors.

According to Pohlman, the active agents in breaking the shell are chiefly the *musculus biventer* and the *musculus spinalis*, which move the head and the upper vertebræ of the neck. During the late stages of development the head is to be seen bent to one side; the muscles in question shift it into one of extension more nearly in line with the vertebral axis. This straightening of the head is responsible in great part for breaking the egg-shell.

Furthermore, the stimulation of the muscles referred to is probably due indirectly to the distension of the abdomen brought about by the complete incorporation of the yolk-sac. This pulls the trigger of a drinking-choking reflex, which is not dependent on a demand for oxygen. It seems that the whole body of the chick suffers from (œdematous) excess of water. This is due to the changes in the yolk-sac and the allantois, to awakened glandular activity, and to insufficient kidney elimination. When hatching makes it possible for pulmonary respiration to begin, the excess of water is soon got rid of, for that is one of the functions of the lungs in birds. The facts also account for the ability of the newly-hatched chicks to go at least three (perhaps four or five) days without water.

Re-investigation of the process of hatching should be made in the light of Pohlman's criticism, but it looks as if the important muscular agency was to be found not in the *complexus* but elsewhere, and that the breakage of the shell is due to efforts to straighten out the head, which has hitherto been bent to one side.

§ 9. NATURAL HISTORY OF BIRDS' EGGS

Enthusiasts on the subject of birds' eggs have invented the word "öology" as the name of their science, and Professor Newton, in approving of this, goes the length of saying that "hardly any branch of the practical study of Natural History brings the inquirer so closely in contact with many of its secrets." He refers to one of the scientific triumphs of the oologists—namely, discerning, from the eggs, what Huxley confirmed anatomically, the affinity between the Limicolæ (snipes and plovers) and the Gaviæ (gulls and terns). Eggs can be studied as scientifically as anything else, and they have the fascination of great beauty of form and colouring.

Size and Number.—The smallest bird's egg is that of the humming-bird, the largest is that of the extinct *Aepyornis*, which held six times as much as an ostrich's, and a hundred and fifty times as much as a fowl's. It is said that the egg of the extinct *Moa* sometimes measured 9 inches in breadth and 12 in length, but that of *Aepyornis* was far larger. Of European birds, the swan has the largest egg, the goldcrest the smallest. What is the biological significance of the differences in size?

In the first place, there is a *general* relation between the size of the egg and the size of the bird. In the main this means that the egg of a large bird has a large legacy of yolk, for it is on the amount of yolk and white of egg, not on the amount of genuine living matter, that the differences of size mainly depend. It is the nutritive material rather than the formative material that counts; and in a general way we can understand that a big bird requires a send-off of nutriment on a more generous basis than a small bird.

But there are many exceptions to the general correspondence between size of egg and size of bird. Thus the cuckoo is much larger than a lark, but the eggs of the two are about the same size. The guillemot and the raven do not differ greatly in size, but the egg of the former has a volume several times greater than that of the latter.

When a bird lays only one egg, it is likely to be relatively large, as in guillemot, gannet, and puffin, it may be noted that these birds lay in places where enemies are few and where it is not dangerous that the egg should have a conspicuous size. The eggs of the wingless kiwi of New Zealand are larger in proportion to the bird's size than in any other case; and it is interesting to notice that they (usually two) are stowed away in a nest at the end of a tunnel in the ground.

In the case of birds whose young are hatched rapidly and leave the nest very early, the eggs are usually large in proportion. In other words, a relatively large legacy may make for precocious development, which might be very advantageous in some cases and the reverse in others.

Professor Newton remarks that the number of eggs to be covered at one time seems also to have some relation to their size. Those of the snipe are equal in size to those of the partridge, but the partridge is a much larger bird than the snipe, therefore the snipe lays four while the partridge may lay a dozen. The snipe could not cover more than four, and, besides, it will cost the snipe more to produce four than it will cost the partridge to produce four. Now if the number of eggs bears some relation to the risks of juvenile mortality, as seems generally true, and must yet be regulated in reference to the number the bird can cover, we see how the size of the egg might be determined, within limits, in the course of natural selection.

Observations in the poultry yard and comparisons of the habits of different birds certainly suggest that a highly nutritive, sluggish, anabolic bird will have larger eggs than a relatively more active bird with a sparser diet. Variations in constitution would be naturally correlated with diversities of size and number, and these diversities would afford materials for natural selection. Those constitutions in which the size and the number of the eggs suited the conditions of life would become racially fixed.

We have noted that the eggs of ground-nesting birds are in most cases relatively large, and that this may be reasonably associated with the advanced state of the young when

they are hatched. Mr. Edward J. Bedford gives the following illustrations: "The Common Snipe and the Blackbird are about the same size, and while the average size of the egg of the former is 1.58 inches by 1.1 inches, that of the latter is only 1.18 inches by 0.85 of an inch. The Curlew, Raven, and Guillemot are all about the same size, and while the average measurements of the egg of the Raven are 1.95 inches by 1.3 inches, that of the Curlew is 2.65 inches by 1.85 inches, and the Guillemot 3.25 inches by 1.95 inches."

Shape.—Most eggs are obviously oval, and this shape is related to the conditions of muscular pressure within the oviduct before the shell consolidates. In owls and some other birds the eggs are approximately spheres, and this is a retention of the shape of the ovarian egg. Those of the sand-grouse are almost cylindrical with obtuse ends; those of grebes are wide in the middle and equally pointed at the two ends so that they approach a biconical shape. In fowls and the like there is great variety in the precise shape, and strange abnormal freaks are not uncommon. In a large collection of eggs with many examples of the same species the variability of shape within narrow limits is very evident, and we understand again that in the course of time there may have come about by selection a fixing of the fittest shape. This is not inconsistent with the determination of the shape by the conditions of pressure in the oviduct, for these depend on the structure and constitution of the hen-bird—likewise subject to variation.

It is probable that the shape of the enshelled egg is most important in relation to the process of being passed down the lower part of the oviduct and laid. The broad end is always first. But there are cases where another utility may be recognised. Thus in the eggs of most *Limicolæ* (snipe, plover, and their relatives) there are four eggs which lie with their narrow ends almost touching in the centre, so that there is economy in the space to be covered by the brooding bird.

Darwin pointed out that the single egg of a guillemot or a razorbill is laid on the narrow shelf of a precipitous sea-cliff. It is liable to be jostled by the wind or by the parents'

feet. But its shape is such that it does not readily roll, it rotates on its minor axis within a very limited radius. In this case the shape may be secondarily justified by saving the egg from tumbling into the sea. A guillemot that varied in the direction of a spherical egg would not be likely to start a new species! But it must be kept in mind that auks are affiliated to plovers, so that the top-like shape was probably a legacy from the ancestral stock.

Shapes of Eggs.—The factors which determine the shapes of the eggs of birds have been discussed by Professor D'Arcy W. Thompson (1908), who points out that in dealing with organic forms, we should try to interpret them in terms of "the intrinsic forces of growth acting from within and the forces of tension and pressure that may have acted from without."

The problem is : given a practically incompressible fluid, contained in a deformable capsule, which is either (*a*) entirely inextensible, or (*b*) slightly extensible, and placed in a long elastic tube, the walls of which are radially contractile, to determine the shape under pressure.

An incompressible fluid contained in an inextensible envelope cannot be deformed without puckering of the envelope taking place, and, as this does not occur, it may be assumed that the envelope is in some measure extensible, or that the whole structure grows under relatively fixed conditions—two suppositions which are practically identical with one another in effect.

At all points the shape is determined by the law of the distribution of radial pressure within the given region of the oviduct, surface friction helping to maintain the egg in position. Professor Thompson then proceeds to explain that if the egg be under pressure from the oviduct, but without any marked component either in a forward or backward direction, the egg will be compressed in the middle, and will tend more or less to the form of a cylinder with spherical ends, as hinted at in the eggs of sand-grouse (*Pteroclidæ*).

When the egg is subject to the peristaltic contraction of

the oviduct during its formation, then, from the nature and direction of motion of the peristaltic wave the pressure will be greatest somewhere behind the middle of the egg; in other words, the tube is converted for the time being into a more conical form, and the simple result follows that the anterior end of the egg becomes the broader and the posterior end the narrower. Extreme forms of this are seen in the pointed egg of guillemot or razorbill.

Texture.—In some families of birds the shell has definite physical characters of grain or texture or gloss—an illustration of *specificity*. A kind of bird may sometimes be identified from a single feather, and a fish from a square inch of its skin, and a tree by a single leaf. A species has usually individuality even in details—thus the blood of a horse can be distinguished from that of a donkey by the shape of the blood-crystals; and sometimes the peculiarity extends through all the members of the family. Though it may not be of much vital importance, it is an index of blood-relationship. The egg of the cuckoo is often almost indistinguishable in colour and markings from the eggs of the foster-parents' clutch, but it is usually distinguishable in its texture.

The fine-grained white shell of the kingfisher's egg has a beautiful gloss and opalescence: what a contrast to the rough chalky surface of the grebe's! The strangely coloured egg of the Tinamou is like "highly burnished metal or glazed porcelain:" what a contrast to the pitted surface of the eggs of South African ostriches, or the rough surface in the Solan Goose! In many water-birds, like ducks, the surface of the shell is oleaginous, which may have some value in keeping them from being over-wetted. Instances might be multiplied, but it would serve little purpose, since the biological significance of the differences in texture is obscure, and may indeed be minimal. Professor Newton calls attention to the fact that the egg-shells of hybrids between Grey and Black Crows (probably varieties of one species) are distinguishable in texture from those produced when the two forms pair with others like themselves.

The shell usually shows two layers—an inner or mamillary which is always without pigment except in the Anis (*Crotophaga*), and an outer or spongy which may or may not be coloured. Outside this there is often a pellicle or skin-cuticle. As has been mentioned, the shell is porous and there is an indispensable interchange of gases between the developing embryo and the outside world. In at least some pelicans and penguins the shell is still flexible when the egg is laid; but this simply means a certain prematurity in laying, and need not be connected with the flexibility of the shell in some Reptiles. In all birds the shell passes through a flexible phase.

Why should Eggs go Bad?—It does not seem so easy as one would think to answer this simple question. Out of 2520 fresh eggs examined by Philip B. Hadley and Dorothy W. Caldwell (1916) there was bacterial infection in the yolk of 8.7 per cent. None of the 111 whites examined showed any infection. The bacterial types were cocci, bacilli, and spirilla, but it did not appear that they were of much importance. They probably infected the eggs in the ovary, having escaped from the intestine into the portal circulation. According to the investigators this primary infection plays no rôle in bringing about the decomposition of eggs nor in causing embryo-mortality. Why, then, do eggs go bad? For the factors determining decomposition secondary infections must be looked to, and we suppose that the microbes must either enter through the pores of the shell or must be included about the shell-membrane and shell while these are being formed in the lower part of the oviduct of the hen. The use of "egg-glass," lime-water, and the like for preserving eggs is to close up the pores of the shell, excluding both microbes and air.

Coloration.—Droplets of pigment are secreted from the lower part of the wall of the oviduct, and these stain the egg-shell before it has finally set. The staining may be diffuse, or well-defined spots may be fixed when the egg remains for a time stationary. As the egg may move onwards before the secreted pigment is fixed—before the paint is dry—there

arise long streaks, hair lines, and smeared splashes. That the pattern is often very pleasing every one admits.

The pigments are related to those of the blood and the bile, *e.g.* oorphodein and biliverdin respectively; but their primary meaning remains obscure. It is very likely that they are unimportant by-products or waste-products of the bird's metabolism, which are got rid of along with the all-important nutritive secretions from the wall of the oviduct. The pigments in withering leaves are very beautiful and very striking, but, so far as we know, they are devoid of biological significance except as end-products and by-products in the essential chemical routine of the green leaf.

Three points seem to us of much importance. The first is that of variability. The beautiful collections generously given by Mr. R. Hay Fenton to the Aberdeen University Museum show the extraordinary variety of coloration and pattern in the eggs of guillemot, lapwing, black-headed gull, rook, and cuckoo. To look at a drawer of a score of different kinds is like sitting by a fountain of change, and there are many such drawers. These cases show that it need not be of much importance what colours and pattern the egg has. Within wide limits the secretion in the oviduct may vary, and it is known experimentally that feeding or fright, age or other nurtural conditions may affect the coloration of a bird's egg. If it should become of survival-value that the egg of a guillemot or a cuckoo, let us say, should settle down to some particular coloration, there is plenty of raw material on which the process of natural selection could work.

The *second* point is specificity—that *on the whole* there is distinctive coloration for each species. Those who make a study of birds' eggs do not usually make a mistake, unless they come across some very divergent variation or freak. Each species is itself and no other. Is it not the case that the shell-membrane in the guillemot's egg is almost always yellow, while that of the nearly related razorbill, often alike in external coloration of shell, is green? The specificity may simply mean that a certain type of constitution has been stabilised—similar metabolism,

the same pigments, similar proportions of parts, similar secretory activity, the same rate of oviducal movement, and so on—*therefore* similar results. There is extraordinary variability in the colour of cuckoo's eggs, but there is very cogent evidence that when a cuckoo has begun to lay eggs of a certain colour, she keeps to this.

The *third* point is that the pigment is often hidden from the outside, being deposited in the deeper parts of the spongy layer of the calcareous shell. In such cases it cannot be of much direct use unless as a screen protecting the development of the embryo from certain rays of the sun.

Our argument is that there is no need to search too diligently for the utilitarian significance of the distinctive coloration of birds' eggs. The pigmentation may be a by-play of metabolism and the constancy of pattern an expression of an orderly constitution. And that may be all.

Yet it is not in the least inconsistent with this to inquire whether in particular cases a particular coloration may not have a use and may not have come under the sifting action of natural selection.

§ 10. POSSIBLE USES OF EGG-COLORATION

(1) The eggs of birds that lay their eggs in ground-nests or in exposed nests are often very inconspicuous. About ninety British birds nest on the ground, and in many cases the eggs (and the birds too) harmonise protectively with their surroundings. This is plain in the case of Ringed Plover, Tern, Stone Curlew, and Lapwing. When danger threatens, the alert cock-bird often gives the alarm and the female leaves the eggs, runs along the ground for some distance and then takes wing. But the exposed eggs are not conspicuous; their colouring and patterns harmonise with the ground-scenery; sometimes the gloss reflects the light in a way that makes them still more difficult to discover. We have seen a woodcock's nest with white eggs and the conspicuousness of these was enough to convince us of this at least, that

there are limits of coloration beyond which an egg in a ground-nest cannot pass with any chance of survival.

It is true that unspotted eggs and *not* inconspicuous may be found in exposed nests, but it is often easy to see why this need not be dangerous. Some birds, like pheasants and partridges, draw leaves or other covering over the nest, and this will also help to conserve the warmth. Some birds, like wood-pigeons, sit very close. Some birds are formidable, as in the case of cormorants and herons, and are not much molested.

There are some cases where the resemblance of the eggs to the surroundings is very striking. It is often difficult to avoid treading on the eggs of the tern lying in a scraping on the shingly beach. The eggs of the night-jar harmonise beautifully with the mottled ground amongst the furze. The eggs of the cassowary are large, three inches by six, but their emerald hue matches the moss in the jungle.

(2) The eggs of birds that lay in holes or in covered nests are often white, *e.g.* in kingfishers, puffins, and owls, and this has been interpreted in terms of the fact that in the situations habitually chosen the eggs are not visible to hungry eyes. It might also be said that in such situations, there are no inimical rays of the sun to be screened off. Perhaps a deeper way of looking at it is to say that the absence of shell-pigment is a primitive feature, as seen in reptiles, and that birds which persisted in having white eggs had to seek out concealed places or build well-covered nests. The humming-bird's very white egg is laid in an open nest, but the nest itself is very well hidden among the leaves.

(3) There is attractiveness in McAlldowie's suggestion that the pigmentation of the egg-shell may be of value in screening off certain rays of the sun, which might injure the developing embryo, especially in much exposed nests like those of rooks. The blue-green pigmentation would be especially useful, but what is lacking is experimental evidence. It is not difficult to find cases which McAlldowie's theory does not fit, but perhaps this is not very useful. If the pigmentation be primarily by-play, it may nevertheless be

utilised for secondary advantages in certain cases. That it is not always utilised in this particular way, proves nothing.

Professor Newton referred to the pigeons' white eggs in very exposed nests, to the whiteness of owls' eggs, whether laid in a hole, or on the bare ground, or in an open nest on a tree. The gos-hawk has a white egg, and that of its relative the sparrow-hawk is blotched, yet the nests of the two birds are built in precisely the same kind of position. Such cases prove that it is not a matter of life and death for an egg in an exposed nest to be coloured like a crow's, but they do not rule out the suggestion that pigmentation may sometimes be a useful screen.

The eggs of the snow-bunting are richly and delicately coloured, but they are sedulously concealed beyond the reach of reflected light. This proves that the type of pigmentation has not always any significance as a screen, but it does not prove that the screen theory may not sometimes apply.

(4) The eggs of cuckoos are very diverse in coloration, but it is likely that one and the same cuckoo lays only one type of egg. This is placed in a foster-parent's clutch, and in some cases the resemblance is so close that it needs a practised eye to detect the cuckoo's egg. In other cases, the intruded egg is strikingly conspicuous and challenges attention. Thus there is a very interesting occurrence of resemblance on the one hand and contrast on the other. It would require prolonged investigation to make sure that the similar eggs are more successful than the dissimilar ones. Some foster-parents are more dupable than others, but we do not know whether colour-resemblance in the eggs makes the duping easier. The mother-cuckoo is often very deliberate in her choice of a foster-nest, but we do not know whether this is in any way determined by the colour of the egg she lays. We do not know whether she appreciates the colour at all. It is certain, of course, that she cannot change the colour at will, and that she is *not* "maternally impressed." But our ignorance far exceeds our knowledge of the cuckoo, and most other things.

§ 11. FERTILITY AND FECUNDITY

Comparatively little is known in regard to the fertility of birds and the conditions which cause it to vary. Most of what is known is due to the investigations of fowls by Professor Raymond Pearl and his fellow-workers. The maximum total number of chicks physiologically possible to a mated pair is one thing, and the actual number of viable chicks is another, the relation of the actual to the possible is called by Pearl (1917) the reproductive or fertility index. It diminishes after the first breeding season.

In mammals it seems that fertility, starting at a low point at the beginning of the sexual life, rises to a maximum at a certain age, and then declines with further increase in age, until total sterility results. In the fowls Pearl (1917, A) worked with, the rule was very different. There is in both sexes a steady and progressive decline in fertility after the first breeding season. It is more rapid in the male than in the female. "There is a significant drop in reproductive ability as we pass from a combined age of two years for the mated birds to three years. In passing from three years to four there is no significant change in reproductive ability; on passing from a combined age of four years to that of five years, there is a large drop in the net reproductive ability of the mating."

The female's capacity for producing offspring is called fecundity; the actual number produced indicates the *fertility*. A hen may fail to lay anything like the number of eggs which she is capable of producing. She may not be as fertile as she is fecund. A reliable estimate of this fecundity can be obtained by counting the number of readily visible immature ova (öocytes) on the surface of the ovary (Pearl and Schoppe, 1921). For when the ovary is removed it is seen to be like a bunch of grapes. It is made up of many öocytes held together by connective tissue and bound to a stalk which keeps them in position in the body. There are many immature ova which are quite hidden, many that will

succumb to a sort of struggle for existence that goes on in the ovary (Hansemann, 1912), and it may be that many mature ova have been already discharged, but Pearl and Schoppe find that the number of readily countable ova is a reliable index of the fecundity of the bird.

Fecundity is a *variable* constitutional quality, and it is also *modifiable* by changes in nurture. That is to say, it may change for innate or intrinsic reasons, and for environmental or extrinsic reasons. The egg-laying capacity of hens is partly a question of breed and partly a question of food and environment. The reproductive capacity is often delicately poised. It is well known that while gallinaceous birds breed readily in captivity, hawks will seldom do so. Canaries have become fertile in captivity, while finches seldom lay. Darwin remarked on the fact that whereas the female Jungle Fowl (*Gallus bankiva*) lays only six to ten eggs, and the wild duck about the same, the domestic descendants of these birds lay huge numbers in the course of the year. The domestic duck may lay a hundred eggs and the hen two hundred. On the other hand, the guinea-fowl has retained her natural number (14-16), and lays in a hidden nest.

Fowls which lay a very large number of eggs, say 200 in the year, have been obtained by selective breeding from stocks which showed a persistent capacity for being prolific. This illustrates innate fertility. On the other hand, a great increase in the number of eggs laid has been secured for a time by peculiar dieting. Thus Houssay (1903) has shown that a carnivorous diet results in a great increase in the annual yield of eggs, and the second carnivorous generation may be more prolific than the first. This illustrates a modificational increase in fertility, which does not last.

Herbert Spencer advanced the generalisation that Individuation and Genesis vary inversely. When it costs a great deal of energy to keep the individual life going, there is less to spare for producing new individuals. This conclusion was advanced as an induction from a survey of the animal kingdom and mankind; and it seems to be in a broad way true that animals with a highly pitched life, with complex

behaviour and many interests, are less prolific than types with an easy-going life, with abundant food and sluggish habits. But this may simply mean that variations in the direction of economised reproductivity were eminently successful when there were simultaneous variations in the direction of, let us say, keener wits and stronger parental care. But Spencer thought of the correlation as having a direct physiological basis, and this conclusion is less secure. In reference to the familiar fact that moulting hens cease to lay, he said : " While they are expending so much in producing new clothing, they have nothing to expend for producing eggs."

Spencer's contrast between the fertility of birds and mammals is very interesting. " Comparing the large with the large and the small with the small, we see that creatures which continually go through the muscular exertion of sustaining themselves in the air and propelling themselves rapidly through it, are less prolific than creatures of equal weights which go through the smaller exertion of moving about over solid surfaces. Predatory birds have fewer young ones than predatory mammals of approximately the same sizes. If we compare rooks with rats, or finches with mice, we find like differences. And these differences are greater than at first appears. For whereas among mammals a mother is able, unaided, to bear and suckle and rear half-way to maturity a brood that probably weighs more in proportion than does the brood of a bird ; a bird, or at least a bird that flies much, is unable to do this. Both parents have to help ; and this indicates that the margin for reproduction in each adult individual is smaller."

It seems to us that the diversity of fecundity cannot be interpreted very satisfactorily in terms of what surplus there may be after satisfying the claims of individuation. The nexus is more indirect. The bat is uniparous not because it spends so much energy in flight, but because variations in reduced fertility were congruent with the flying habit (for a single young one is enough for the flying mother to carry before and after birth), and were favoured because of con-

temporary variations in the direction of increased parental care. The divergences in the number of eggs in the nests of birds are not interpretable in terms of individual income and expenditure ; they have been slowly wrought out in the course of ages in relation to the broad issues of life.

§ 12. STERILITY

The significance of sterility is very obscure, and we cannot do much more than indicate the various phenomena to which the term is applied : (a) *somatic* sterility, where the defect is not a fundamental inability to produce germ-cells ; (b) *modificational* sterility, where the reproductive organs cease to produce germ-cells because of some deteriorative influence ; (c) *variational* sterility, where the reproductive organs never produce germ-cells, or effective germ-cells, although all the natural conditions are normal ; and (d) *gametic* sterility, where the germ-cells are incompatible.

Somatic Sterility.—The researches of Maynie R. Curtis and Raymond Pearl (1915) make it possible to distinguish “somatic sterility” in fowls (due to some obstruction or disturbance) from constitutional or variational sterility due to some defect in the inheritance. Somatic sterility may be caused by some obstruction in the oviduct or a general lowering of the physiological tone of the individual so that no yolk is formed. In some cases it is impossible for the ovum to enter the oviduct ; it has to pass into the body-cavity, where it is absorbed. An interesting detail is that if there be a stoppage in the oviduct at any level, the tracts on each side of the block pass through the normal cyclic changes, co-ordinated with cyclic changes in the ovary.

Modificational Sterility.—A cessation in the production of germ-cells may be brought about by some drastic change of diet, such as feeding fowls on flesh ; or by some poisoning ; or by some subtle changes such as are involved in confinement. Obviously the absence of willingness to pair, often exhibited by captive birds, must be distinguished from something deeper, namely a stoppage of germ-cell formation.

Variational Sterility.—This term may be used for those cases where the reproductive organs do not produce germ-cells or efficient germ-cells. There is an inherent defect, and it is often seen in hybrid offspring. Whether it is something *per se*, or whether it should be ranked with other germinal variations and mutations is a question too difficult for our present knowledge.

A female bird may be infertile in various degrees, as A. Chapellier has shown (1911) in regard to hybrids between male goldfinch and female canary. The ovary may produce no ova or very small ova; the ovary may produce ova which are not laid or which are non-fertilisable. Twenty different hybrid females have been studied by H. Poll (1911), who finds that complete sterility in the female is marked by the absence of small reserve follicles in the adult ovary and by various signs of ovarian degeneration. There are hybrids, however, which lay eggs and there are a few which lay eggs that develop.

In a study of the spermatogenesis of hybrids between male wild pigeon and female domestic dove, Geoffrey Smith found (1912) that the ripe spermatozoa showed in certain cases structural abnormalities, and were on an average twice as large as the normal spermatozoa of either parental type. All the spermatozoa were probably impotent; these and similar hybrids are invariably sterile. Inquiry showed that the stumbling-block occurred during the maturation of the sperm-cells, and was probably due, as Guyer suggested, to the fact that the chromosomes derived from the specifically distinct parents were incapable of harmonious fusion.

A study of the sterility of hybrid pheasants by Geoffrey Smith and Mrs. Haig Thomas (1913) led to the conclusion that it was connected with abnormalities occurring in the process (synapsis stage) of the maturation of the germ-cells. The spermatozoa of the hybrids are either deformed or abnormally large. The immature ova fail to grow. Similarly, in the case of male hybrid ducks (*Cairina moschata* and *Anas boschas*), it has been shown by H. Poll (1911) that up to a certain point the spermatogenesis in the testes seems normal

enough. But they break down when it comes to forming functional spermatozoa. If these defects in the sex-cells be traced a little further back they may be referred to something incompatible in the chromosome equipment of the parental sex-cells. In some mammals which yield sterile offspring when crossed the *numbers* of the chromosomes in the two parents are too different to admit of the establishment of a successful lineage of germ-cells in the offspring. But there may be other forms of incompatibility besides too great numerical difference between the chromosome groups of the two parents.

Pointing in the same direction are the observations of Professor M. F. Guyer on the male organs of hybrids between cock and guinea-fowl. The testes were well-developed, but no spermatozoa were formed. As in hybrid pigeons there is a critical phase—the synaptic phase—which few of the developing germ-cells (spermatocytes) can get past, the chromosomes of the two parents being seemingly unable to unite normally.

Gametic Sterility.—In a successful cross between birds of different varieties or species, the fertilised egg develops into an able-bodied offspring, but this hybrid may be innately sterile. It may fail to produce any germ-cells at all, or its germ-cells may be non-viable. But there are attempted crosses which do not result in offspring. The ova will not be fertilised by the spermatozoa, or the spermatozoa will not fertilise the ova. This is incompatibility of germ-cells which are normal and vigorous.

The general conclusion hinted at from the facts known in regard to sterility in birds is that it concerns the bearers of the hereditary traits—the chromosomes. Max Morse (1910) gives a cautious expression of this view in the sentence: “All of the studies which have been made point to the conclusion that whatever be its nature, there is an ‘incompatibility’ existing between the chromosomes of individuals of different species or varieties.”

CHAPTER XI

PARENTAL CARE AND NEST-MAKING

- § 1. Incubation. § 2. Nest-making. § 3. Feeding the Young.
§ 4. Educating the Young. § 5. Defence of the Young. § 6. The
Case of the Cuckoo. § 7. The Case of the Mound-Birds.
§ 8. Social Life. § 9. Retrospect on the Evolution of Parental Care.

COMPARED with most fishes and amphibians, and even with most reptiles, birds show a marked reproductive economy. The practicability of this has depended on an associated increase of parental care. It has not been proved that reduction of reproductivity is the direct physiological consequence of an intensification of life, or, to use Herbert Spencer's phraseology, that the reduction of genesis is the result of heightened individuation. What may be safely said is, that a successful line of evolution was entered upon when certain birds varied more or less simultaneously in the direction of reduced reproductivity and in the direction of parental care. Reduced reproductivity left more energy free for other ways of disposing of it, but it would have been a hazardous experiment if it had not been associated with increased parental care, which implies reduced infantile mortality.

There is another way of looking at the matter. When the chances of life are heavily against survival, *e.g.* when enemies are very numerous, the spawning solution is often quite effective. Only a few oyster embryos survive out of a million, but the race of oysters continues because the oyster produces so many millions. Parental care is at once unnecessary and impossible. When parental care made economised reproductivity possible without endangering survival, it likewise made its own growth more possible. With fewer offspring,

kept for a longer time in association with the mother, or with both parents, it became possible for the parents to know their own children and physical bonds of tenderness were established. Thus parental care worked in favour of its own further evolution. The family reduced to small dimensions and kept for a longer time in touch with the parents not only engendered parental affection in the individual, but formed the sieve by which germinal variations in the direction of more parental affection were sifted, thus leading to the evolution of racial virtues. This is one of the indirect ways in which mind may act as a factor in evolution.

§ 1. INCUBATION

Some of the lower Vertebrates (fishes and amphibians) remain in close association with their eggs or keep them in contact with their body. The gunnel on the shore coils round its egg-mass, the male sea-horse carries the eggs in a ventral pouch and the male Kurtus in a double bunch on the top of his head. The Surinam Toad carries her developing eggs in skin pockets on her back ; Darwin's frog (*Rhinoderma darwini*) carries the eggs, few in number, in his mouth. These are instinctive habitudes, but they are probably associated with some degree of awareness ; it is difficult to think of them *originating* without this, though they may eventually become matters of instinctive routine. In some Boidæ the mother snake coils round her eggs and this approaches incubation.

It is natural that the female bird should rest after the exhaustion of egg-laying, and it may be that the nest has in some cases a primary association with the act of mating, but it seems an unworkably extreme view to refuse the brooding bird any appreciative awareness of the eggs as products of her own being. It is certain, of course, that the incubation has become part of instinctive routine, engaged in because of inborn nervous pre-arrangements which operate when appropriate stimuli pull the trigger ; but it is uncertain to what extent the instinctive performance is associated with

the activation of higher nerve-centres, which may imply some degree of appreciative awareness. It is also uncertain to what extent the bird may have acted intelligently or controlledly in ancient days when a new departure in instinctive routine was tested, and either approved of or rejected.

The tendency to brood is a normal element in the cyclical reproductive activities of the female bird, and is wrapped up, in a way not clearly understood, with the activity of the ovary. Normally, in the domestic fowl, the brooding instinct finds expression after laying a clutch of eggs, but it is not necessarily so. Raymond Pearl has shown (1914) that the degree of intensity of the brooding instinct, both in respect of its objective manifestations and of its physiological basis, may vary considerably at different times in the life of the same individual. It is sometimes very persistent; in other cases it disappears very quickly.

It has been shown that a pigeon will fail to notice its eggs if removed to a distance of a foot from the nest, or that another will sit close on a nest without any egg at all; but futility along particular lines is very characteristic of many animals, and it means that the enregistration of certain chains of behaviour may be so thoroughgoing that it approaches mechanisation. When, in natural conditions, there is little risk of anything going wrong with the routine, the more automatic it becomes the more profitable it will be.

It is characteristic of many instincts that they may continue beyond the normal period unless some event occurs which switches them off. This is well illustrated in the case of incubation, and it is not always a disadvantage. In their experiments with Tumbler Pigeons, Leon J. Cole and W. F. Kirkpatrick noted (1915) that when the eggs do not hatch they are seldom abandoned at the end of the normal period of incubation. The birds sit on for an average of six days after the normal period, making the mean total time of incubation (when the eggs do not hatch) twenty-three days after the laying of the second egg. This is a "factor of safety" in the incubating instinct. The number of days required for the young to hatch being variable, "nature,

rather than drawing the line too closely, makes allowance for the extremes." There is an inertia in instinctive behaviour, until things take a new turn.

Surprise has sometimes been expressed that a bird should go on sitting on eggs which are not developing. A turtle-dove is a very sensitive creature, knowing when " a profane hand " has, in its absence, touched the eggs or the young, and leaving them in consequence, yet it will sit for eighteen days on addled eggs. But the expression of surprise is due to a misapprehension of the nature of instinctive behaviour. For we may be sure that the brooding dove is not meditating over its eggs or wondering why nothing has happened, it is bound by promptings which must be obeyed, and which will continue to operate until some internal or external change switches off the current.

A simple adaptation at the nesting time is the suppression of scent in ground-birds like partridges. There is so little scent that a first-rate dog may be taken to within a foot of a sitting partridge without his showing any interest, always provided that the bird is not seen. As birds have no sweat-glands the smell probably comes from the preen-gland or from the cloaca, and it would be very interesting to know how it is suppressed. Tegetmeier, the great authority on pheasants, had a theory which he called " vicarious secretion." He believed that odoriferous particles are normally given off from the bird's skin, but during the brooding, in some way or other, the bye-products are shunted into the food-canal, and got rid of along with the bird's droppings at a safe distance from the nest. But this shunting is obscure. It would be of interest to compare the normal activity of the preen gland with its condition at the breeding season, to see if there is any difference.

The uses of incubation are : (1) to supply from the body of the brooding bird the warmth which furthers the development of the embryo within the egg, a function helped by non-conducting materials in the nest ; (2) to hide the eggs and nestlings from the eyes of enemies ; (3) to shelter the young from the heat of the sun, to which many of them are very

susceptible. Some details are interesting. Thus some birds (*e.g.* albatross, penguin) show bare patches where the eggs come into direct contact with the warm skin ; some brooding birds, *e.g.* snipe, increase their inconspicuousness by putting soil on their backs ; some birds, *e.g.* eider-duck, draw a coverlet over the eggs when they have to leave the nest. These details suggest the danger of easy-going mechanical interpretations.

Mere bare patches require no special interpretation, but there is sometimes a very definite transformation of the skin and blood-vessels, which may be seen, as in the Crested Grebe, long before the time for brooding—in the young bird indeed. The transformation consists in an absence of the fatty layer (*panniculus adiposus*) and in the marked development of a network of blood-vessels. These include the external thoracic artery, the abdominal cutaneous artery, and the abdomino-pectoral cutaneous veins. The significance of this “brooding organ” is that it brings the warmth of the blood nearer the eggs.

The modes of incubation may be classified :—

- (a) Female only, *e.g.* the hornbill, albatross, eagle-owl.
In many cases, as in the hornbill, the male feeds his brooding mate.
- (b) Male only, *e.g.* the emu and the Rhea. In the Grey Phalarope, where the female does the courting, the male does the brooding.
- (c) Both parents, *e.g.* ostrich and oil-bird. In both these cases the female sits by day and the male by night, while pigeons illustrate the ordinary method of irregular alternation.

Brooding of Pigeons.—It may counteract the vagueness of these general statements in regard to incubation to give some details of the behaviour of pigeons, based on the careful observations made by the late Professor Whitman (1919). The time of incubation differs in different species ; in the common pigeon it is 17–19 days, in turtle-doves 14–16 days. In the now extinct Passenger Pigeon it was only 12½ days. Some species begin to sit on the nest before the first egg is

laid ; in other cases incubation may be delayed, or may be very intermittent, until the advent of the second egg. This has an interesting result, that the period required for the second egg is generally shorter, and " the shortening of the time for the second egg secures a greater equality of the two young birds in feeding." This is important because the stronger and better-developed nestling is rather apt to monopolise the nutritive attention of the parents.

Most species of pigeon lay two eggs, but some lay a single egg ; and species that lay two may sometimes lay only one. Even when no egg is laid, the bird may persist in incubation. The first egg is always dropped in the afternoon ; the interval between it and the second egg is variable, but it is very frequently 1 day, 14 hours. In many cases the female pigeon shows diagnostic symptoms before laying : " the wings are held loosely and allowed often to drop below the tail ; the bird looks as if sick, and moves about heavily and with unusual care " ; she may sit on the nest for 3-4 days before laying. The young birds usually hatch in the early morning or forenoon. Rarely or never do they hatch in the afternoon. If the hatching has not occurred by 3 p.m. one may be almost certain that nothing will occur until the next morning. It seems probable that the young bird, within the egg, has its times of resting, which correspond with the times of resting in the parent bird. If a young bird has partly cracked the shell, but has not finished before noon, it may " go to sleep and wait till next morning." The egg-shell is usually first pricked about 24 hours or more before the young bird liberates itself, and the breakage is almost invariably at the larger end. " Both parents exhibit an increase of interest in the nest at hatching-time. This is not necessarily due to the presence of the young, as it may manifest itself before the eggs are hatched."

Both parents share in the brooding. In the pigeons studied by Whitman the female sat during the night, while the male normally roosted on the perch as far from the nest as possible. During the day there is alternation, but the male sits for the greater part of the time. Both parents

often show stubbornness in giving up the nest, and the male may have to force the female off. At other times the sitting bird utters the nest-call as a call for relief, and this is sometimes, but not always, responded to with promptitude. The same call is almost invariably given upon taking the nest, but it is also uttered at frequent intervals and without apparent purpose during the sitting. Normally there is no courting or sexual activity during the incubation, but the male often tries "to break up the cycle."

For a week after the hatching of the eggs the parent birds continue to brood. "At the end of the week the young can be left uncovered for some time without harm, and the period of 'close sitting' characteristic of the incubation period ceases. At the end of the second week the young begin to venture from the nest and become more and more independent of parental care."

The nestlings are first fed on the "pigeon's milk"—the cellular debris regurgitated from the crop of both parents. After the food-canal has been educated on this very digestible material, the young birds receive the partially digested food of the parents. The regurgitation-period lasts for two weeks, and then the young birds, leaving the nest, pick up food for themselves.

In many birds living in natural conditions there is only one brood in the season, but if a disaster occurs to the first brood the reproductive cycle may immediately recommence. In some birds, two broods are normal, and this is common among domesticated and semi-domesticated pigeons. There may be a renewal of the reproductive cycle at the end of the second week, just as the young are venturing from the nest. The female stops feeding and devotes her entire energy to another brooding. "The male continues the feeding and also participates in the incubation of the second set of eggs. When the eggs are hatched, the male devotes his attention to the new set of young, and the first set are forced to rely upon themselves for their sustenance. 'Driving' is sometimes necessary to accomplish this weaning of the first young. If a series of cycles follow each other in immediate

succession, the male bird will thus be continuously engaged in the task of feeding his various broods of offspring" (Whitman, 1919, p. 63).

§ 2. NEST-MAKING

Birds are not the only animals that build nests. The male stickleback glues together the leaves or fronds of water-weed and the lampreys make a nest of stones. The squirrel makes a big nest in the trees, and the harvest-mouse fastens its cradle to the stems of corn. Among insects also there are many constructions which might be called nests. The wasp's hanging house of paper serves also for the deposition and hatching of the eggs, and for securing the safety of the young during the period of nurture. But the word "nest" always suggests the word "bird," and that is obviously because brooding is characteristic of birds and a nest is an auxiliary to successful brooding.

The *uses of nests* are mainly (1) to conceal and shelter the eggs and the young and the brooding bird; and (2) to make brooding easier and more effective. Sometimes the nest has a prior significance as a pairing platform; sometimes its depth is advantageous in keeping the nestlings from premature excursions. Sometimes, when the collection of non-conducting material is large, the dominant function is that of keeping up a suitable temperature around the eggs and the imperfectly warm-blooded young ones. A good example may be found in the feather nest of the eider-duck. In other cases, when the outside of the nest is carefully decorated with lichens and even gossamer, the function of concealment is emphasised. The thorny sticks in the large domed nest of the magpie suggest defence. In short, the character of the nest varies as this or that function is emphasised.

Specificity.—Within narrow limits of variability, usually traceable to lack of materials, the type of nest is specific. A particular kind of bird builds a particular kind of nest and, as a rule, no other. Blackbird and thrush are near relatives, but their nests are quite different. Examples of plasticity are known, but the main fact is specificity, and this points

to ingrained instinct. Thus we are assured that a greenfinch, incubated by a canary in a canary's nest, made, in the course of time, a true greenfinch nest of fibrous roots, moss, wool, and horse-hair.

There is often considerable elasticity in the choice of a site. The Golden-Eagle usually nests on a ledge of the cliff, but it may choose a tree. Herons typically nest on high trees, but they may elect to build in an open fen. The noble falcon whose eyry is typically on the beetling cliff may nest in a marsh. Bird literature is full of instances of similar plasticity, which are more interesting than cases of building inside a station lamp or up the sleeve of a scare-crow, for it is often forgotten that these curious sites have not to birds anything of the significance they have for man.

Methods of Building.—The *modus operandi* in nest-building can hardly be described in general terms. The bird uses its bill and its feet, twining and twisting the materials together. When the nest begins to take shape the bird may get inside and turn round and round. The hens usually do most of the nest-making, but the cocks often collect materials and may share in the work more intimately. In the case of pigeons the cock may be seen bringing straws to the female who has already begun to sit; he mounts on her back and passes the straw over her head within reach of her mouth. This suggests a slight overlap of the incubatory period by the more strictly sexual period.

To appreciate the making of nests without hands, it is necessary to take detailed instances. The house-martin presses the tiny daubs of clay against the wall and hastens slowly, for much must not be added till what has been already built has hardened and set. In making their leaf nest the male and female tailor-birds work together; she gets into the middle of the two or three drooping leaves, he remains outside; holes are made through the leaves and threads of fibre are passed in and out—a literal sewing. The fantail warbler is said to knot the thread with which it sews the leaves together, and it also forms a canopy of grass-stems above the nest.

Birds with no Nests.—In many birds the labour of nest-building is scamped or shirked. Thus the tern makes no more than a mere scraping on the sand or shingle, and the same is true of divers, thick-knees, and sand-grouse. Razor-bills and guillemots place their single egg on a bare ledge of rock, where its shape gives it some chance of not being knocked over or blown over into the sea. The stone-curlew and the night-jar make no nest nor any preparation of the soil, and yet year after year they come back to the same spot.

A slight improvement may be seen in many of the gulls, sandpipers, and plovers. They lay their eggs in shallow hollows in the ground, but as incubation proceeds a breast-work of stems and leaves may be added. Many ducks are about the same level; they make a slight depression and line it sparsely with down—the first hint of the thick quilt made by the eider. The ringed-plover usually lays its eggs in the shingle, where they are most effectively lost to ordinary vision, and Professor Newton calls attention to the interesting point that when the bird breeds on grass uplands it still paves its nest with small stones—the ways of the past living on in instinctive promptings even when they have ceased to be relevant.

In not a few birds the only care is to bury the eggs, which recalls the habit of many reptiles, such as crocodiles. The female ostriches scrape holes in the sand and bury their eggs, but they also incubate during at least part of the day. The males sit at night. The Kiwi of New Zealand puts its single, relatively large egg in a hollow among the rhizomes of the tree fern. Some of the Megapods or Mound-birds bury their eggs in the sand and leave them to hatch by the heat of the sun, but others heap a huge hotbed of dead leaves over the spot. This may be 5–6 yards high and 10 yards round, and many mothers share in its making. Alfred Russel Wallace noted that the mother mound-birds may come from a distance of 10–15 miles to suitable places in Celebes, near hot springs, for instance. They make their mound, lay their eggs, and depart, for there is no food for them. The

quill-feathers of the chicks are sometimes so long that they can fly at birth, so everything works well.

The mounds of the mound-birds, where part of the warmth is due to fermenting vegetation, suggest the masses of vegetation gathered by grebes and some rails. The birds do not shirk the patience of brooding in their half-floating nest, but they seem to trust partly to the heat of decomposition. It is interesting to think of this inter-regnal co-operation, an inter-twining of threads in the web of life, for the Bacteria which are so often the minions of death are here helping indirectly to foster young life.

Nests in Holes.—From burying it seems natural to pass to burrowing, and there are many birds that lay their eggs in holes or tunnels, the excavation of which is more or less their own work, though the holes of rabbits and the like may also be utilised. At the end of its long tunnel the sand-martin makes a scanty bedding of roots and feathers collected from far and near. The kingfisher makes in its hole a strange nest of undigested fish bones. Rabbit-holes are sometimes utilised by sheld-duck, even to a depth of ten feet or more, but the bird also burrows of itself. The puffin may utilise a natural hole or it may burrow in loose soil.

Just as some birds find a hole in the ground and utilise or improve it, while others make the hole themselves, so it is in regard to holes in trees. The woodpecker carves out a hole in the decaying stem, while the nut-hatch usually finds a hole and improves upon it by plastering up the entrance so as to leave only a narrow doorway and by collecting the scales of cones and fragments of bark to make a dry bed within. A nut-hatch may have 10,000 tiny pieces of bark in its nest, which represents a prodigious industry.

The climax in the way of utilising holes in trees is seen in the hornbills. A hole may be deepened if it is too shallow or its floor may be raised if it is too deep. In some cases the powdery dry earth obtained from the broken-down hills of the termites is utilised for the bedding. The female, who is weak and moulting at the time, enters the hole, and the male narrows the doorway with resinous stuff and other

materials mixed with salivary juice, so that would-be intruders are readily baffled. On the male falls the responsibility of providing food for his imprisoned mate, and by-and-by for the single nestling as well. He brings food-materials—fruits and seeds and insects, often enclosed in a thin skin like that of a sausage, which turns out to be a product of the lining of the gizzard from which the food is regurgitated. The female bird becomes fat, but the male sometimes dies of exhaustion, especially in bad weather.

Platform Nests.—From nests or apologies for nests on the ground, one might pass to the earth-mounds made by flamingos, or in another direction to rough platform nests like that of the wood-pigeon, which is often so slight that the white eggs may be seen from below. From a rough stick platform there is a gradation leading to the more elaborate constructions made by rooks and crows. Improvements on this are seen in the fence of thorny sticks which magpies build and in the sparse internal bedding gathered by bittern and heron.

Nests of Earth.—Deserving a place by themselves are the solidly built nests, such as the swallow's—generally like half a saucer, built of mud mixed with short straws, and made comfortable inside with a lining of feathers and fine grasses. An improvement on this is made by the house-martin, for the mud nest is shaped like half of a deep cup and is closed in except the doorway at the top or corner of one side. There is a lining of feathers, which the martin catches in the air, and pieces of straw. The nest of the South American oven-bird (*Furnarius*) is nearly as big as a football and weighs 8-9 pounds; it is made of mud mixed with a few sticks and straws, and shows an elaboration in being divided into two rooms, an ante-room and an egg-room. It is a big, massive nest, but it is built pellet by pellet by a bird with a tiny bill.

Extraordinary Nests.—Some of the Passerine birds use their saliva to moisten or glue the fibres or tiny twigs with which they build their nest, and this habit points on to the extraordinary nest of the sea-swift *Collocalia* of the Far East which is made of consolidated salivary juice. The nest is

shaped like a shallow saucer and is fixed against the vertical walls of cliffs and caves. Those of the first quality look rather like frosted sugar and consist chemically of mucin for the most part. They form the stock of the Chinese Bird's



FIG. 46.—The sea-swift (*Collocalia*) and its edible nest. From a specimen.

Nest Soup, and it is said that $3\frac{1}{2}$ millions used to be sent from Borneo to China in one year. When the nest is taken the bird may make another of inferior quality, yellow rather than white in colour, and obviously eked out with seaweed.

Feltwork Nests.—Some of the most beautiful nests are of the feltwork type familiar in the case of chaffinch and goldfinch. With a basis of interwoven fibres they may be lined with hair or feathers, and disguised externally with moss and lichens and spider's web. They are open in the two finches named, domed in the wren and bottle titmouse, slung like a hammock in gold-crest and oriole, suspended by a string in certain grosbeaks and humming-birds. These nests have two good qualities: they must be very comfortable and they are well camouflaged. In the nest of the long-tailed-tit there is a feltwork of lichens, moss, wool, and spiders' webs and a quilt-like lining of small feathers, whence the name "feather-poke." It is an elongated oval with a small doorway in the upper part of one side. A suggestion of the labour involved in this elegant construction is given in MacGillivray's record that he counted 2379 feathers in one nest.

Among the feltwork nests there are many individual touches of great interest. Thus there is no doubt that the light nest is sometimes weighted with lumps of clay. Certain warblers (*Aedon* and *Thamnobia*) invariably place a piece of snake's slough on their nest, like the horse-shoe above the house-door.

The Psychological Aspect.—Without further experiment it is not possible to go far with the analysis of the bird's behaviour in nest-making. (a) The theory that the bird behaves as a Robinson Crusoe might do, who tried to build a hut, never having seen one before, is extremely improbable. In the first place, because the architecture of the nest is so *specific*; in the second place, because there is *so little tentativeness* or hesitation in the bird's behaviour. The behaviour of the builders does not suggest the activity of intelligent artists picking and choosing their material and testing its capacities.

(b) Alfred Russel Wallace lent his great authority in support of the view that intelligent utilisation of tradition and models counts for much in the case of nest-building. While a bird may inherit an indefinite tendency to use its energies in this direction, how it builds and when it builds

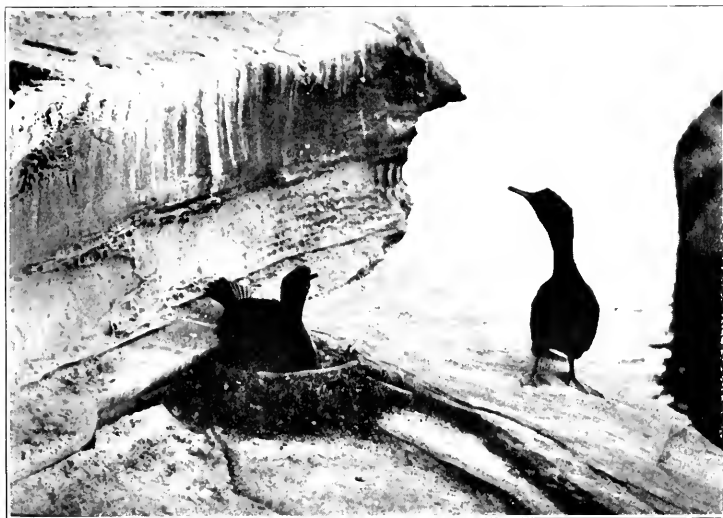
PLATE VII



[Photo by Rattar, Lerwick.

NEST OF EIDER DUCK, (*Somateria mollissima*).

This is made of down-feathers plucked by the bird from its own body.



[Photo by Rattar, Lerwick.

NEST OF SHAG (*Phalacrocorax graculus*).

On the low shelf of a sea-cliff. The female on the nest.

depends on the extra-organismal tradition of the species. The tradition includes the imitation of previous and contemporary nest-builders. The nest-building may thus be compared to the preparations that a human mother makes for the birth of a child : she has not only an instinctive but an intelligent awareness that some provision of garments is necessary, but it will probably be admitted that this would not be very effective without the guidance of social tradition. As a matter of fact, external guidance is so copious that there are few data to indicate how much could be done by individual reflection or how much would be done instinctively without deliberation at all. Man cannot get back to such detachment from the social heritage ! As to birds, Wallace brought forward little evidence beyond cases where birds transported to a novel environment built a new kind of nest. Chaffinches taken to New Zealand no longer made the typical chaffinch nest ; but it is necessary to know how far the deviation was due to changes in the available materials.

(c) A third view is that the nest-building is in the main instinctively determined. That is to say, the bird has a hereditary pre-disposition to go through a certain routine, without much or anything in the way of education or experience, requiring only a succession of liberating stimuli to pull a succession of triggers. On this view, the bird is an *instinctive artist*, working as the inherited spirit and flesh move it to work, following a series of inborn promptings or inspirations. This is very different from intelligence ; it is physiologically like a concatenation of reflex actions. This does not, however, exclude the possibility that the physiological concatenation is suffused with awareness and backed by endeavour.

(d) But even if the manner of the nest-building is in the main instinctive, the expression of inborn or hereditary structural pre-arrangements within the nervous system, and of some measure of psychological awareness associated with these, it does not follow that no importance should be attached to individual intelligence or learning ; it does not follow that no importance should be attached to imitation and tradition.

In his "Habit and Instinct," Professor Lloyd Morgan comes to the conclusion that "nest-building in definite ways is an instinctive activity; but that it is modifiable by individual experience."

The "false nests" made by various birds are probably due to slight aberrations or exuberances of the nesting instinct. It seems too generous to interpret them as deliberate devices for leading enemies astray. The so-called "cocks' nests" of redshanks are "little depressions scrubbed out on the ground with a few bits of rushes and grass roughly arranged in them. They look like the work of a 'prentice hand—of a redshank who was lacking in experience, and was trying to get his 'hand in' before taking to the serious work of nest-building."

It is interesting to notice the psychological change that marks many birds during the nesting time. Round about a strong colony of Black-Headed Gulls at the time of brooding the visitor is met by little troupes which do not disguise their displeasure. Redshanks, surely of a more pacific temperament, fly to meet the intruder and sweep close by him quite fearlessly.

§ 3. FEEDING THE YOUNG

Those young birds that are hatched at an advanced stage of development (*Præcoces*), as in the case of lapwing and chicks, begin very early to fend for themselves. Yet every one is familiar with the way a hen calls her chickens to the morsels she scratches up, and many have watched a swan feeding the cygnets with weed from the bottom of the lake. But when the young birds are hatched as helpless nestlings (*Insessores*), the labour of feeding them is great. In the majority of cases the male does more than his share, and it is an interesting fact that some males, *e.g.* snipe, that absent themselves during the brooding, return to duty when the young are hatched.

As it is important to realise that many living creatures spend a large fraction of their time and energy in furthering

the welfare of the young, it is of real value to have records like that given by Professor Robert Newstead, who calculated that a single pair of Great Tits destroyed between seven and eight thousand caterpillars during the twenty days occupied in rearing their young. What a quaint picture some of the Antarctic explorers have given us of the penguins toiling up the steep ice-cliff with their crops heavily laden with small shrimp-like Crustaceans (*Euphausidæ*) which they have collected for their offspring—sometimes so heavily laden that they lose it all in the course of their climb !

Some peculiarities in connection with the feeding of the young deserve careful consideration. Certain birds of prey hunted off their nest will drop food on their young ones. Male and female pigeons give their squabs a readily digestible creamy fluid which serves, like mammal's milk, for the education of the food-canal. This "pigeon's milk" is not a secretion of the walls of the crop, for these are non-glandular ; it is produced by a fatty degeneration and internal moulting of the cells lining the crop. A curious case is that of the Storm-petrel, the well-known bird of the open sea, which only comes to land to breed. The parent bird sits close on the single egg, which is laid in a hole among the rocks, or perhaps in the disused burrow of a rabbit. When the young one is hatched out, the parents seem to leave it all the day long, for they are nervous of the land. They return to it at nightfall, however, and give it a heavy, lasting meal of oil from their crop—apparently the concentrated essence of many minute crustaceans and other small fry of the sea.

The parent puffins brood on their single egg for about a month, and for as long again the fluffy youngster requires to be fed. Both the parents share in the labour of love, and it is a familiar sight to see them bringing in small fishes, several at a time, held crosswise in the mouth. As many as eleven have been counted in one mouthful, and there are often four or five. It is an old puzzle how the number of fishes can be added to without loss of previous captures ; perhaps the solution is to be found in the grip of the tongue

and of some spines in the mouth. The feeding of the young obviously involves a great expenditure of energy, for it is often necessary to fly several miles before the fishing-ground is reached. This is simply one instance out of hundreds, which lead us to agree with Cresson (1913) that there has been inadequate appreciation of the amount of time and energy that parent animals, and birds very notably, expend on securing the welfare of the young. We have read that on a long summer day a pair of Blue Tits spent sixteen hours in bringing over a thousand caterpillars and grubs to their hungry nestlings.

There are some interesting adaptations on the part of nestlings that make feeding easier. In many cases, especially when the parent birds have to go to and fro hundreds of times in a day with tiny mouthfuls of insects, it is very important that the moment of feeding should be as brief as possible. So the nestling opens its mouth, not voluntarily, but reflexly (as we draw back our finger from something very hot) when its bill is touched with the food its parent brings. It is highly probable, as Mr. W. P. Pycraft suggests, that the occasionally bright colour of the nestling's mouth may facilitate the precision of the parent's touch, especially in dim light. Fumbling is out of the question, and we can understand from this simple case how an apparently trivial variation (in this case a brightly coloured mouth) might have survival-value and be established in the course of the struggle for existence.

There is no end to the subtlety of parental-care adaptations. How fit it is that young woodpeckers, hatched out in a deep hole in a tree, should have their juvenile claws and muscles particularly well suited for clambering up to the entrance, thus to receive with the least possible loss of time what their parents bring.

Besides keeping the nestlings hidden, warm, and well fed, the parent birds have a more commonplace task which only a few neglect—keeping the nest clean. They often remove the voided matter in their bills, an operation made easier by a thin pellicle of mucus, which forms a sort of

delicate bag. They may even hold the young ones in such a position over the edge of the nest that all fouling is avoided. Nature is all for health !

There are, of course, some repulsive nests, like that of the beautiful hoopoe, smelling of ordure, rancid butter, ammonia and milk. This must surely be deliberate ; in any case it is an exception that proves the rule. And there is no doubt that the rule is that the parent birds should scrupulously remove all trace of foulness from the nest, and sometimes from the vicinity of the nest. This instinctive piece of behaviour has been established in the course of time not merely in relation to health, but to conceal the whereabouts of the family.

§ 4. EDUCATING THE YOUNG

The experiments of Lloyd Morgan and others have shown that young birds (in some cases at least, *e.g.* chickens) have not many ready-made or inborn capacities of effective behaviour, not many when they are compared with ants or bees. Thus the newly-hatched chick, undoubtedly thirsty and willing to swallow drops of water brought to its bill, will walk through a saucer of water without becoming aware of its significance. If it happen to peck its toes when it is standing in water, it becomes aware and drinks, raising its bill to the sky. But it has no instinctive knowledge of water as such, nor even of the meaning of its mother's cluck if it has been hatched out in a mechanical "foster-mother." What it lacks in the way of inborn instinctive endowment, as compared with a bee or an ant, it makes up for by its power of rapid "learning," its marvellous educability. Hence the importance of the instruction which many parent birds give their young.

The solicitous mother-hen teaching its chickens to scratch and peck, and teaching them also what certain calls mean, is an image of many. There is often direct instruction as well as apprenticeship in flying and diving, in catching prey and avoiding enemies. The peregrine-falcons and

some other birds of prey appear to give their young ones lessons in flying and in the chase. The Great Crested Grebe gets its youngsters on its back and dives, thus forcing them to become at home in the water. It is interesting to learn (Heinroth) that before ducklings leave the nest the mother anoints their plumage copiously with the oily secretion of the preen-gland, so that they are not wetted when they take to swimming. Ducklings which have been hatched out by a hen have not this advantage, but they learn to attend to their foster-mother's calls, though this is not natural for ducks.

It is necessary to distinguish cases where the young birds learn by association to attend to certain parental calls, from cases where they require no instruction, but obey instinctively without knowing why. Thus the young redshank or the young partridge squats at a particular signal from its parent; and remains motionless until another call breaks the instinctive spell.

After the parent guillemots have fed and fondled their single offspring for a month or so, the time comes for its initiation to marine life. Before the young bird is able to fly it may be jostled off the cliff-shelf into the sea, where it is at first greatly embarrassed. But the first step is sometimes taken in a gentler way, for good observers have seen a parent guillemot carrying its young one down to the water on its back, and this is likely to be the case when the cliff is several hundred feet high. A third method of initiation is vouched for, that the parent sometimes seizes its offspring by the neck and carries it down. In any case the young guillemots have to be accustomed to the sea before the time of migration comes, when restlessness seizes the myriads and the cliffs know them no more for half a year.

There are several points of great biological interest in connection with the instruction given by parent animals to their offspring. (1) It is the analogue of tradition and education in mankind. It is a way of entailing gains that do not form part of the organic or germ-plasmic inheritance. (2) The clash of life against environing difficulties and

limitations brings about the struggle for existence. The ways of meeting the difficulties and limitations are many, *e.g.* intensified competition, change of habit and habitat, prolific multiplication. But we must not leave out increased parental care and intensified parental instruction. Variations in these directions have their survival value like variations towards sharper claws, stronger flight, and an increased clutch of eggs. (3) But the improvement of parental instruction secures not only the survival of the offspring, but *better* survival. The young creature gets a better send-off on the adventurous voyage of life.

(4) But this is not all. If a fish has a million eggs many of which become larval fishes, parental care is unnecessary, and it is obviously impossible. But fishes that have only a few eggs, like sticklebacks, for instance, must exhibit parental care, else they would have been long since wiped out. And it is plain that fishes like sticklebacks and seahorses are vastly more interesting creatures than cod and herring. Now in the higher reaches of the animal kingdom, among birds and mammals, this is still more true, and when the offspring are well cared for, when they are not too numerous to be known and loved, the result is not only success to the new generation, but an enrichment of the life of the old.

(5) In this and similar discussions it may seem at first glance as if we argued in a circle. Animals with increased fineness of nature, including kin-sympathy, practise parental care and may educate their young, which in turn enhances the parental nature. We believe that evolution works in circles or in spiral curves in which the ascending line bends back into and intersects a lower line.

If a bird is a sympathetic and enthusiastic parent it will succeed with a small family; but having a small family—knowable and lovable personally—will tighten the parental cords of affection. We do not suppose that this tightening of the individual cords will be entailed on the next generation, yet it will make for success as brood succeeds brood. It will afford the liberating stimulus for all the intrinsic kin-sympathy there is in the inheritance; and enhanced

reproductive success will make for the survival of the emotional altruistic type.

§ 6. DEFENCE OF THE YOUNG

Few birds have much chance when the nest is directly attacked, unless indeed they can enlist the help of their neighbours to drive off an intruder, as cliff-swallows a hawk. There are cases, however, where vigorous defence of the nest is attempted. The cormorant resents an intruder's approach to the nest on the sea-cliff shelf, hissing violently and lunging with its formidable beak. Some of the birds of prey strike even at man, and a swan puts up a strong defence. Black-Headed Gulls and lapwings fly close to one's face, if one draws too near the nest, and the eider-duck has a very unpleasant way of expressing her resentment at being disturbed, or, at any rate, her visceral excitement in the flurry.

When defence of the nest is quite out of the question because of its position or because of the nature of the bird, recourse is sometimes had to wiles. The redshank is extraordinarily successful in leading one astray, and the devices of the lapwing are familiar. Very remarkable is what looks like feigning lameness or a broken wing; if it is not a trick, it is almost uncannily like one.

In rare cases the parent bird has been known to shift its eggs, the goatsucker taking them in its capacious mouth. A transport of nestlings to a place of safety has been occasionally recorded, as in woodcock and eagle-owl. The question of how the woodcock carries its young ones has been discussed at great length, it is probably correct to say that they are pressed between the thighs and that the long bill may also be used to steady them.

Among gregarious birds like geese the presence of the father is said to be of great advantage in securing fair-play for the young birds at the feeding-places. Without a paternal champion they are apt to be killed or starved. Even the timid hen will sometimes wax valiant, and her

gathering of her brood under her wings, for protection as well as for warmth, is as eloquent as it is familiar.

§ 6. THE CASE OF THE CUCKOO

This seems a suitable place for a brief discussion of the astonishing case of the Common Cuckoo, famous for its evasion of parental responsibilities. The main facts are these. The cuckoo is polyandrous, one female pairing with several males. The eggs are laid at unusually long intervals; they are numerous and large for the size of the bird; they are very variable in colouring, but one female probably produces only one type. With considerable stealth the mother-cuckoo foists its egg into the nest of some other bird, usually insectivorous, such as hedge-sparrow or meadow-pipit, the number of different kinds of dupes being over a hundred. If the nest be suitable she may lay her egg therein, or she may lay her egg on the ground, lift it in her bill, and place it quickly in the nest. With few exceptions only one egg is placed in a nest. Of great interest are the careful observations of Mr. Edgar Chance (1922), who has proved that in some cases the cuckoo *lays* her egg in the foster-parents' nest. But there are nests in which this is impossible.

In a small percentage of cases the coloration of the cuckoo's egg closely resembles that of the foster-parents' eggs, but this does not seem to be important. If it should come to be of survival value that the cuckoo's egg should have a particular coloration, there is an extraordinary wealth of variations on which Natural Selection might operate.

The egg of the cuckoo tends to develop more rapidly than that of the foster-parents, and thus the nestling cuckoo is able to oust the foster-parent's eggs or young ones. For some eleven days after hatching it has a curious hollow on its back which works well in the "dog-in-the-manger" behaviour. Moreover, the young cuckoo is ultra-sensitive to contact; the touch of another young bird sends it into almost epileptic convulsions, and it is very strong for its

size and age. It gets the nest all to itself, and it is attended with fatuous diligence by its foster-parents, who may continue their attentions even after it leaves their nest. The adult cuckoos leave Britain some six weeks before the young ones, so that the latter must make the southward journey without any help from their own kindred.

The riddle of the cuckoo's behaviour has not been wholly read, but there are three considerations that make it less mysterious than it seems at first sight. (1) It is not a unique phenomenon; it occurs in many other species of cuckoo and in the quite unrelated Cow-Birds; at least one species of Oriental cuckoo is parasitic in one part of the country and nests in another; many different kinds of birds utilise the nests of their neighbours either as a practice, as in one of the ducks (*Metopiana peposaca*), or as an occasional aberration.

Hilzheimer notes that the Great Spotted Cuckoo (*Coccyzus glandarius*) lays several eggs in the nest of a crow or some related bird, and that the young cuckoos do not try to oust the rightful tenants; that *Scythrops novæ hollandiæ* keeps to the nest of one of the "Piping Crows" (*Strepera tibicen*); that some other cuckoos make a joint nest; and that in some other forms both parents brood normally. It is important not to confine attention to the highly evolved case of the European Cuckoo (*Cuculus canorus*).

(2) The mother cuckoo is a bird of many peculiarities. She is polyandrous, and the parasitism is congruent with that; she is very prolific, often laying ten or a dozen eggs; her egg-laying is strangely interrupted, which would not fit in well with personal incubation. Moreover, cuckoos feed very largely on hairy caterpillars which become scarce after midsummer—an economic reason for the early migration and for leaving the care of the young to others.

(3) Most light, however, is to be got from Professor F. H. Herrick's suggestion that the loss of the nesting-instinct is due to an irregularity in the rhythm of the life-cycle—a formula which covers many a variation among animals. Just as one kind of bird may build supernumerary

nests, so the cuckoo may build none. Just as the courtship period, which normally stops as brooding begins, may be lengthened out abnormally, so the cuckoo may shorten down its brooding to nil. A lack of time-keeping or attunement between egg-laying and nest-building is casual in many birds; it occurred as a variation in the ancestors of the European Cuckoo and became established as a racial peculiarity because it was congruent with some other peculiarities of constitution and habit, and because it was found to work well.

§ 7. THE CASE OF THE MOUND-BIRDS

Incubation may be skipped altogether, but this does not necessarily imply the absence of parental care. The most instructive case is that of the Mound-Birds of Borneo and other parts of the Far East, technically called megapods (*Megapodius*) because of their heavily built legs, which are capable of very vigorous digging.

One of these birds, the maleo of Celebes, often makes its nest in the dry volcanic sand near the shore. A pair of them dig a hole about a yard deep and a yard in diameter, and in this the mother-bird lays an egg and covers it with sand. They then return to the forest. At intervals, however, extending over a considerable time, they come back to the shore, and the hen lays egg after egg till there are eight or more. Then the hole is filled up and the precious pair retire for good to the shelter of the trees and trouble no more about the matter. There is perhaps no food for them near at hand, and in any case there is no need for them to stay. The warmth of the sun-baked dry sand is sufficient to ensure the development of the embryo, and the sand is loose enough to let air in to the eggs. It must be an awkward place to be born in, beneath the ground, but the young mound-birds manage to struggle out safely. Some young mound-birds are unique in being able to fly on the day of their birth, but it is said that the young maleos are only able to run. In any case, running or flying or both, the newly hatched

malcos make for the shade as quickly as possible. It is not unscientific to wonder if parents and young ever meet. There must be some need for introductions.

The strange name "Thermometer Bird" is given to a South Australian mound-bird (*Lipoa ocellata*) whose behaviour makes a fitting climax. The birds choose a clearing in the low bush, where there is loose sandy soil, and the clearing must be open to the sun (to the north or east), and it is usually protected by bushes from the prevailing wind. Taking time by the forelock the two birds begin operations long before the actual breeding season. (1) First of all, they dig a circular pit about a foot deep, piling up the scratched-out earth in an outer rampart. In the circular pit they make a heap of withered leaves and other parts of plants, the collecting of which means very heavy work and terrific scratching even for a megapod. (2) The next step is to suspend operations. The collection of leaves and twigs is left for four or five months to soak in the rain, and it begins to decay. (3) But after a while a third chapter begins. The birds make a firm nest or egg-chamber in the centre of the compost-heap. It has walls of interlaced twigs and fibres, and a floor of mixed sand and plant-remains, what might almost be called vegetable mould. Over this a mound of leaves and twigs is piled up till it stands about a yard high and has a diameter of perhaps four yards. Sand is thrown all over it, the whole business involving much time and much hard work. (4) The fourth chapter begins six to nine days after the completion of the mound. The builders return to the scene of their prolonged labours and open the mound carefully, making a gallery near the top, so that the internal nest is reached. In this nest the hen lays an egg, fixing it upright, broad end up, in the mould, and staying it with twigs. Then the mound is made tidy and off they go. Every three or four days, about nine o'clock in the morning, they turn up at the mound and open it up again to get at the nest, in which the hen puts another egg. At length there are about fourteen eggs, in three tiers, four or five in each tier, all in the same position, and all securely

fixed. If the arrangement is disturbed by some intrusion, the mother-bird puts it right again. Non-brooder though she is, she is very punctilious in her parental care. After each egg-laying the mound is, of course, carefully closed up. (5) Eventually it is left more or less alone, though the birds keep an eye on it all the time. The heat of the sun promotes fermentation among the leaves—Bacteria helping Birds—and the temperature sometimes rises to over ninety degrees Fahrenheit. If the weather is very warm the temperature of the mound is apt to rise too high, but the birds attend to this by opening up and loosening the material around the egg-chamber. It is to this extraordinary carefulness that they owe their name “Thermometer Bird.” They are also careful to secure good ventilation, for the embryos would die if there were not plenty of air in the nest. The fact is that they do die of suffocation if some accident befalls their parents and the hill becomes sodden. (6) The young birds have a prolonged development of about forty-five days within the egg, and they are very vigorous when they are hatched. They wrestle upwards out of the egg-chamber and out of the mound, and make for the bush with all haste. If anything should stop them, say fatigue, in the process of wrestling out of the mound, they die. For if an instinctive activity is coercively stopped, it does not usually recommence. If the birds get safely out they are still in considerable danger from enemies, until they are able to get off the ground on to the trees, which must be a great relief.

This is only a glimpse of the mound-bird's story, but we have said enough to show that a bird which does not incubate may nevertheless show a wonderful subtlety of parental care.

There are different kinds of mound-birds and different expressions of the parental care. In some cases a great mound of vegetation is made and used jointly by several mothers. In all cases there is the associated adaptation on the part of the young birds that they are precociously vigorous when hatched. Some, as we have mentioned, are able to fly away the day they are hatched. This illustrates what may be called a “temporal variation,” in other words,

a lengthening out or a telescoping down of particular arcs on the normal life-curve. In the mound-birds there is a lengthening out of the ante-natal period and there is a telescoping down of the nestling period to a vanishing point. Both in cuckoo and mound-bird there is on the parent's part a suppression of incubation, but could there be a greater divergence in the associated tactics which secure the welfare of the young?

Biologically regarded, the facts of parental care among birds are in three ways of surpassing interest. (1) They illustrate a subtle mingling of instinctive routine and intelligent plasticity. (2) They show how economised reproductivity may be made feasible by an elaboration of parental care. (3) They convince us that in the struggle for existence the collecting of feathers to line the nest—to take a diagrammatic instance—may have survival value as real as beak and claws. When we appreciate the nest-making and the brooding, when we think of the feeding, the education, and the defence of the young, when we inquire into aberrant cases like that of the mound-birds (surely balancing cuckoos!), must we not admit that birds spend a large fraction of their time and energy in activities not directly self-preservative, but in the interests of their offspring. If so, animal evolution has its ethical note.

§ 8. SOCIAL LIFE

Many birds are gregarious, but not many are social. When suitable breeding-places are not very numerous, those that are available may be congested, as in the case of shelved cliffs which are densely crowded with gulls, guillemots, razorbills, and the like, or in the case of swampy ground near a loch which is thickly covered with the nests of black-headed gulls. But there is no corporate life in such cases, though it must be admitted that the mere force of numbers may have a protective value against birds of prey even when there is no concerted action.

A social note is struck when there is some measure of

combination against attack. Coues reports having seen little cliff-swallows nesting in the immediate neighbourhood of the prairie-falcon. Kropotkin refers to this case in his "Mutual Aid" (1904, p. 35): "The little peaceful birds had no fear of their rapacious neighbour; they never let it approach their colony. They immediately surrounded it and chased it, so that it had to make off at once." So wild duck will unite their forces in driving off an eagle, and wagtails a hawk. The bold lapwing will fly close to an intruding enemy and summon its neighbours to its assistance. Brehm writes of the common lapwings: "To see them attacking a buzzard, a kite, a crow, or an eagle, is one of the most amusing spectacles. One feels that they are sure of victory, and one sees the anger of the bird of prey. In such circumstances they perfectly support one another, and their courage grows with their numbers" (quoted by Kropotkin, "Mutual Aid," 1904, p. 25). The same sort of concerted action is familiar in many other birds, such as gulls and terns.

The social note becomes more definite among birds which move about together in flocks, like the herds of mammals, for there may be leaders and sentinels and other suggestions of division of labour. This may be illustrated by cranes and flamingoes, by parrots and the crested "American partridge" (*Lophornyx californicus*). In some cases several sentinels are posted when the flock is feeding, and it is almost impossible to take them by surprise.

Another less frequent feature is exhibited by pelicans, namely co-operation in the quest for food. Of the pelicans it is said that "they always go fishing in numerous bands, and after having chosen an appropriate bay, they form a wide half-circle in face of the shore, and narrow it by wading shorewards, catching all the fish that happen to be enclosed in the circle. On narrow rivers and canals they even divide into two parties, each of which draws up on a half-circle, and both wade to meet each other" (quoted by Kropotkin, "Mutual Aid," 1904, p. 23).

Co-operative sociality is also suggested by the Republican Birds, where there is combination in building a big common

nest in a tree—a huge structure which looks from a distance like a Zulu kraal.

Perhaps the climax is to be found in the most familiar case, that of the rooks and their rookery, a case the more remarkable since, apart from the jackdaws, the other members of the crow tribe are solitaries and individualists. There may be far over a thousand nests in a rookery; the same site may be used for more than a century; there is a sort of objective enregistration since the old nests remain for a long time in evidence and may be used over again; there seems to be some utilisation of sentinels; there is some indication of social conventions, for after a nest has reached a certain stage its materials are not stolen. As every one knows there is much talking and clear evidence of several different “words.” There are gambols and sham-fights, frolics and wild chases—in other words, a good deal of play.

Finally, as we have already noticed, there is often a very distinct social note in *migration*. No one dare say much about “social tradition,” but it is noteworthy that many birds which insist strongly on privacy and rights of “territory” in their summer quarters are very social when they undertake their journey southwards. This is seen in the preliminary massing, in the excitement of the crowd, in the trial flights, in the gregarious journeying, and in the utilisation of leaders.

§ 9. RETROSPECT ON THE EVOLUTION OF PARENTAL CARE

The organic starting-point is carrying the eggs before birth. In many cases, *e.g.* crabs, spiders, some fishes and amphibians, but not in birds, of course, the eggs are carried after they are laid.

On another line is viviparity, which occurs at many levels, where the eggs are hatched, as it were, within the body, and where there is sometimes a more or less intimate partnership between the unborn young and the mother. Some reptiles show this, but this path was not followed by birds.

PLATE VIII



[Photo by Kattar, Lerwick.

THE TWO NESTLINGS OF THE GREAT SKUA (*Catharacta skua*).
They are buffish brown. The "egg-tooth" is seen at the tip of the bill.



[Photo by Norrie, Fraserburgh.

GULL'S NEST RAIDED BY A SKUA (*Hoy, Orkney*).

The eggs are broken and their contents devoured.

As the eggs of birds are not carried about after they are liberated, and as there is no viviparity in birds, an expedient is to bury them in the ground—as ostriches and some mound-birds do. Some reptiles do likewise. The mother crocodile sometimes lingers near the place where she has buried the eggs and digs them up when the young are ready to hatch out. This lingering near the spot points the way to brooding, and that again begins with reptiles, as is illustrated by the python.

But brooding on the ground is tedious and risky, and there is a long inclined plane of nests which give the parent bird more comfort and safety and make the hatching out more successful. A prolongation of development and of the period of infancy was possible in a nest safely hidden in a tree, and it may have been that this favoured the evolution of a large and plastic brain—not too heavily endowed with instincts to be *educable*.

But greater success in rearing the family make a smaller clutch possible, and a tightening of the cords of love. Emotional bonds were forged—a premium was put on the sympathetic type. Family life began, often with some education, occasionally with some short-lived comradeship. And some birds went beyond this to the level of sociality.

CHAPTER XII

SENSES, INSTINCTS, AND INTELLIGENCE

- § 1. The Eye. § 2. The Ear. § 3. The other Sense-Organs. 4. The Inclined Plane of Animal Behaviour. § 5. Instinctive Behaviour. § 6. Intelligent Behaviour.

It is convenient to consider the senses along with the behaviour of the bird. All living means activity, and part of this is *agency*, when the organism acts on its environment. If this acting is to be effective, the creature must be aware of its environment; and the sense-organs are the "receptors" of the stimuli which form the raw materials or data of the awareness. They are the gateways of knowledge. The Golden Eagle must have a very precise estimate of the position of the grouse if it is to clutch it in its talons without ceasing to fly, and the Osprey must have an even more difficult problem with the swimming fish.

Even when there is no emphatic agency, the sense organs are indispensable in the adjustment of the organism to its environment. They are needed for reactions as well as for actions. The brooding bird, oppressed by the heat of the sun, will turn in its nest so that it secures some relief. In cold weather the internal production of heat is automatically increased so as to compensate for the loss of heat into the frosty air. In both cases the adjusting reactions follow the stimulation of sensitive nerve-endings in the skin. We see, then, that through its sensory system the bird actively tests the outer world and is also more passively recipient of surrounding influences.

How many different kinds of sensory "receptors" there are it is difficult to say, for besides eyes, ears, olfactory

membrane, touch-spots, and taste-spots, there are nerve-endings particularly sensitive to changes of temperature and pressure, and it may be that there is a magnetic sense. But sight and hearing seem to count for most in the bird's intensely active life.

§ 1. THE EYE

The eye may be usefully compared to a camera, the convergence of the rays of light being effected by the lens and the cornea, the sensitised photographic plate being represented by the retina. The densely pigmented choroid outside the retina makes the back of the eye a dark chamber. The firm and tough external layer of the eyeball, the sclerotic, is a supporting structure. The contraction and expansion of the iris diaphragm in front lessens and increases the amount of light that enters the camera. The region in front of the lens and iris is the anterior chamber of the eye, containing aqueous humour. The region behind the lens is the posterior chamber and filled with vitreous humour. The lens is moored by a suspensory ligament made up of many fibres that radiate from the partly muscular ciliary processes which project inwards at the junction of cornea and sclerotic.

Birds have a very mobile neck, with practically universal freedom of movement, and it is therefore unnecessary that there should be great mobility in the eye. The usual six eye-muscles are reduced and the spherical shape of the eyeball, adapted to ready mobility, is departed from. It often looks as if the eyeball were made up of the parts of two spheres of different radius, a smaller anterior corneal region, usually very convex and often asymmetrically turned towards the nostril, and a larger posterior region turned inwards and backwards. The nearest approach to the spherical shape is seen in the ostrich and in some high-soaring birds of prey; there is often much flattening, as in swan and parrot; there is a constriction and elongation of the median portion and a protrusion of the anterior

portion in owls, Golden-Eagle, and some other predatory birds. The eye is adapted for horizontal vision, and every one has seen a hen turn her head through a right angle to get a glimpse of something overhead.

Some of the detailed peculiarities of the eye are of much interest. The cornea, which is usually very convex, is in some cases particularly strong, probably a protective adaptation. This is very marked in some diving birds, and also in crows and diurnal birds of prey. The eye may

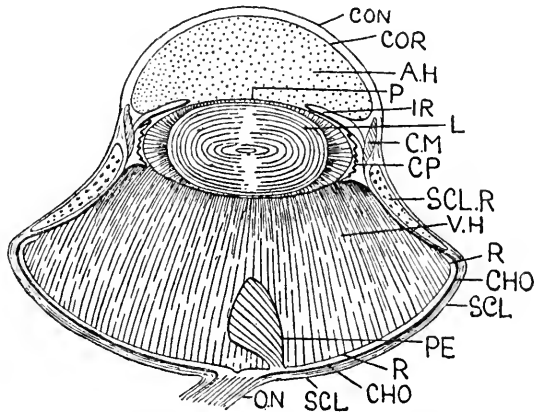


FIG. 47.—Diagrammatic median vertical section through a bird's eye. CON., conjunctiva; COR., cornea; A.H., aqueous humour in the anterior chamber of the eye; P., the pupil, surrounded by the iris (IR.); L., the lens; C.P., ciliary processes fastened to the lens; C.M., ciliary muscle; SCL.R., sclerotic ring of bone; V.H., vitreous humour in posterior chamber of the eye; R., retina or percipient layer, innermost; CHO., the black vascular choroid; SCL., the firm sclerotic, outermost; PE., the pecten, projecting into the vitreous humour; O.N., the optic nerve.

thus be strengthened against the pressure of deep water or against the concussion of branches. Strengthening of the eyeball is also effected by a ring of bones at the anterior margin of the sclerotic where it joins the cornea—an interesting ring because it occurs also in some reptiles, and is a tell-tale evidence of the reptilian origin of birds. In many there is a narrow posterior embasement of small bones where the optic nerve enters the eye.

The cornea consists of two lamellæ which are movable on one another. A muscle, called Crampton's, runs from a circular ridge on the outer margin of the inner lamella to the margin of the sclerotic ring. The contractions of this muscle flatten the periphery of the cornea and cause the central portion to bulge outwards. Another muscle, called Müller's, extends from the circular ridge of the cornea into the choroid, and other fibres pass into the ciliary processes which are closely united with the surface of the lens. In a complicated way the various muscles combine in adjusting the focus of the eye for different distances, and in this function birds excel all other animals. The most important point is that this power of accommodation in birds is twofold, partly by altering the lens (as in other Vertebrates), and partly by altering the curvature of the cornea.

There is strong contractility in the mobile pigmented iris which forms a diaphragm-like membrane in front of the lens, with the pupil in the centre. In other Vertebrates the musculature of the iris is smooth or unstriped, which means relatively slow contraction; but in birds the muscle-fibres of the iris are striated or striped, which means rapid contraction. In accommodation the iris is pressed firmly by its circular muscles against the front of the lens, and there is, for the time being, no communication between the anterior and the posterior chamber of the eye.

The important general point is that birds surpass all other creatures in their power of rapid accommodation. With great rapidity and ease they can change the focus of their eyes from that suited for seeing a near object to that suited for seeing something at a distance. As Mr. Beebe says, the bird's eye "in a fraction of time can change itself from telescope to microscope." At one moment the hen is anxiously scanning the sky lest a carrion crow is near; next second she is inspecting a minute insect larva among the dust at her feet and picking it out for her chickens.

Besides the musculature for altering the curvature of the lens and the cornea, there is a remarkable development

of elastic tissue, and Professor E. W. Carlier (1906) has pointed out that there is relatively more of this in birds than in any other animals. It occurs in the sclerotic, the choroid and various other parts of the eye, and there is also, as hinted at in lizards, a special elastic tendon for the insertion of the ciliary muscle. Now the adaptive significance of this relatively strong development of elastic tissue in the eye is not far to seek. Professor Carlier notes that birds and reptiles are the only Vertebrates with striped muscle fibres within the eyeball, and this is particularly marked in birds which have such powers of rapid accommodation. The powerful and rapid contraction of the muscles would give a shock to the delicate structures within the globe and might interfere with clearness of definition, but there is a means of absorbing this shock, and of converting the sudden pull of the muscle on the choroid into an even, continuous strain. This is effected by the great increase in the amount of elastic tissue within the eye.

If it be asked why birds should excel other animals in power of accommodation, the answer may be found in their rapid flight from far to near, and in the fact that optical alertness means everything to them. In its rapid plunge on its quarry how quickly the bird of prey must alter its focus!

The colour of the bird's eye is determined by various conditions (see Bond, 1919). (1) Thus there may be no pigment on the anterior surface of the iris, and the black of the posterior or uveal epithelium shines through the translucent anterior and results in a black or dark eye—the "bull" eye. (2) There may be no pigment on the anterior surface of the iris, yet the iris may not be translucent owing to its being crowded with colourless granules, which prevent the passage of transmitted light, but when seen by reflected light give the iris a grey-white appearance, the "pearl" eye. (3) The anterior surface of the iris may show a network of branching cells crowded with small yellowish granules, and this results in the "yellow" or "gravel" eye. (4) Many birds have on the anterior

surface of the iris a network of cells with dark brown or black pigment, resulting in a black eye very different from the "bull" eye (1). (5) Matters become more complicated when there are two kinds of pigment on the anterior surface of the iris. There are some remarkable special cases. Thus in Lawes' Bird of Paradise a brilliant colour effect is produced by a combination of three factors: (a) a translucent iris which allows the uveal pigment to shine through, (b) the absence of anterior yellow pigment-cells in the inner zone of the iris, and (c) a fibrillation of the connective-tissue in that area which acts as a diffusion grating and causes light reflected at a certain angle to appear blue.

In the percipient layer or retina which lines the interior of the back chamber of the eye, there is in our eye a small area of acutest vision, the yellow spot or *fovea centralis*. The highly complicated retina is here thinned down to the percipient elements known as the rods and cones. In owls, whose eyes look forward, with axes parallel to one another, the central fovea is absent, and its place is taken by a temporal fovea. The same is true of the Oil-bird, *Podargus*.

In birds that pick their food from the ground, like curlew and wagtail, and in swimming birds, like ducks and geese, there is a horizontal fovea and a central one as well. In quick-flying birds there is a temporal fovea and a central. In the swift, the swallow, and the tern there are three foveæ, so that the finest flight and the most complex retina go together.

Very characteristic of the bird's eye is the pecten, a vascular pigmented fold, protruding into the vitreous humour of the posterior chamber. It arises from near the "blind spot" where the optic nerve enters the eye and divides into its many branches. It varies greatly in size, sometimes reaching almost to the posterior surface of the lens, sometimes being very inconspicuous. It is rudimentary in the Nankeen night-heron (*Nycticorax caledonicus*), but it is never absent—not even in the Kiwi (*Apteryx*), as has been stated.

Various functions have been ascribed to this pecten. It has been regarded as a light filter, protecting the retina from too intense illumination. It has been credited with regulating the transference of fluid from the anterior chamber to the posterior chamber of the eye when there is focussing for near vision, and it is certainly well-developed in high-flying birds, birds of rapid flight, and birds of prey where the accommodation of the eye has to take place very rapidly. And it is small in nocturnal birds. Against this view is the fact that the pecten occurs in some reptiles.

Dr. Lucas notes that a strongly developed pecten creates a large blind area in the eye, for it is heavily laden with dark pigment and the rays of light that fall on it are naturally absorbed. "This explains to some extent the constant shifting of the head when the bird is on the watch, as the visual field is considerably limited, the portion obstructed being toward the upper outer field of vision."

A very careful study of the pecten has been made by Ebba von Husen (1913), who comes to the conclusion that it is mainly concerned in the making of the vitreous humour. The tissue of the pecten is a network of coalescent cells, like the neuroglia cells which form the scaffolding for nervous tissue. But the pecten is not nervous or sensory. It is covered with epithelial cells with their bases turned outwards; there is fluid in the intercellular spaces of the network of anastomosing cells; there are also blood-vessels.

In development the pecten starts, as Berndt has shown, from a mesodermic keel and an ectodermic covering, both of which contribute to the making of the embryonic vitreous humour. In this way the pecten will aid in the nutrition of the eye and will assist in regulating the tension.

It must be pointed out that some investigators insist that the pecten is a definitely nervous structure. Thus V. Franz (1908) is most circumstantial in his declaration that the pecten is not a derivative of the choroid, but of the optic nerve. Apart from the blood-vessels which arise from the ophthalmic artery, the pecten, according to Franz, consists entirely of nervous tissue, and bears sensory pro-

cesses on its surface. Franz regards it as an intra-ocular sense-organ, serving for the perception of the fluctuations of pressure in the vitreous humour which arise from the movements of the lens in accommodation.

Little seems to be known in regard to the colour-sense of birds, and experiments are not very easy. Thus, if certain birds do not pick up seeds coloured blue, it does not follow that they do not see them; it may simply mean that they have formed no association between a blue object and food. Erna Hahn (1916) found that some parrots, *e.g.* *Melopsittacus* and *Cyanospiza*, seemed unable to become accustomed to take their food on an area illumined by coloured light. Fowls, on the other hand, picked up blue seeds and uncoloured seeds in a blue area; they made no use of those in ultra-blue or ultra-violet areas.

The use of brightly coloured pods and flowers by Bower-birds suggests a colour-sense, and so do the bright colours of many male birds, but it is always difficult to distinguish what may be discrimination of colour from what may be only discrimination of differences in the intensity of the light reflected from the surface.

The experiments of Hess on fowls, pigeons, and birds of prey show that birds' vision and man's are practically the same towards the orange-yellow end of the spectrum (long wave-lengths), but that birds' vision falls far short of man's towards the blue-violet end. In fact, birds cannot see blues and violets. Hilzheimer notes that our vision would be like a bird's, as regards colour-perception, if we wore reddish-yellow glasses.

The retina or sensitive surface shows the usual nerve-endings, known as the rods and cones, but the cones are relatively few in number. Cones are believed to have chiefly to do with colour-sensation, and the rods with the discrimination of form. The sensitising substance, the so-called "visual purple," found in the retina, changes under the influence of light and the resulting chemical changes stimulate the nerve-endings, with sensation as the result. In the retina of birds there are red and yellow oil globules, of

unknown function, which do not seem to occur in other animals.

The high degree of visual acuteness in birds is essentially due to the delicacy and dense arrangement of the elements in the restricted centre of the fovea or foveæ.

As regards eyelids, birds have three. The upper and lower eyelid meet when the bird is sleeping, but in ordinary cases they do not move nearly as much as man's do. In our case the upper eyelid is frequently drawn down over the front of the eye, moistening and cleaning the surface of the eyeball, and overlapping at the outer corner the lower eyelid which comes up a little way to meet it. In birds the lower eyelid comes far up. Mr. Beebe notes that in the Great Horned Owls the action of the two lids is much the same as in man. The upper and lower lids are fused in the very young bird until near the time of hatching or for some time after.

Of great interest is the third eyelid, which made its appearance in reptiles, and is well-developed in the crocodylians. It is a very important cleaning and protective structure in birds, and is always being flicked down over the surface from the anterior upper corner where it lies. It is pulled down by two special muscles with delicate tendons, and jerks back by its own elasticity when the muscles relax. As it is semi-transparent, the bird can to some extent see through it when it is drawn down for a considerable time, as in an owl which has ventured abroad in the daytime. The old story of the eagle renewing its sight by looking at the sun may have reference to the fact that the bird draws down its third eyelid when looking up into the bright sky, and discloses its keen eye when it turns again from the glare.

This third eyelid is present in most mammals and has an eye-cleaning function. It is absent in whales and dolphins where its rôle is discharged by the continual washing of the front of the eye with water. It is vestigial in man and monkeys, where the upper eyelid has become much more mobile than it is in lower mammals. In man it is

dwindling away, but it is larger in some races than in others, and it occasionally shows a minute internal cartilage, a tell-tale evidence of man's filiation to a mammalian stock in which the third eyelid was large and useful.

Birds have, like crocodiles, well-developed lachrymal glands, but it is rare for them to shed tears. Mr. Beebe describes a flamingo "weeping copiously" in fear of a condor ("The Bird," p. 211). The secretion of the lachrymal gland exudes below the upper eyelid, is spread over the cornea, and drained away into the nasal chamber. There is also a pair of Harderian glands, whose secretion escapes below the third eyelid.

In most birds the eyes are placed very markedly to each side of the head, and the right eye looks to the right, the left to the left. This gives rise to monocular vision, and it is plainly very different from the state of affairs in man and monkeys where the axes of the two eyes are both directed forwards. The advantage of monocular vision is that it allows those birds that have always to be on the look-out two extensive visual fields.

Dr. Lucas writes: "The moment an object of interest is detected the bird does not direct both eyes toward it, but there is a concentration of one eye, the vision of the other being suppressed at will. In some diseases of man, where the axis of one eye has departed from the parallel of the other, each eye sees a field which does not correspond with the other, yet diplopia, or double vision, is not present, as the one or the other field of vision is suppressed according to the automatic concentration in one or the other eye. Note a group of pheasants or pigeons watching the same object; one eye only will be directed toward the position. Watch a fowl or a pigeon gazing upward at a hawk; one eye will be skyward, the other toward the ground. In such cases the vision of the downward eye is being suppressed. If suppression were not possible in birds a condition similar to diplopia would be present. An idea of this condition can be gained by pressing one's eye, thus shifting the visual axis of one eye, when a double image is obtained." Some

people cannot shoot or look down a microscope without forcibly suppressing the vision of one eye by closing it, but it is possible by effort to learn to suppress the vision of one eye while both are kept open.

True binocular vision is familiarly illustrated by ourselves, where two images of an object are formed, each on the same half of each eye. In such a case there is what is called partial decussation of the optic nerves, which requires a little explanation. In all animals from fishes to man the optic nerves cross one another (in a chiasma) before entering the brain. In bony fishes all the fibres passing from the right eye pass to the left side of the brain, and all the fibres from the left eye pass to the right side of the brain. This is called the decussate condition and it is unique. In other cases the crossing of the optic nerves is more intricate—for some of the fibres from the right eye go to the right side of the brain, though most go to the left; and some of the fibres from the left eye go to the left side of the brain, though most go to the right.

§ 2. THE EAR

In contrast to most mammals, birds have no external trumpet or pinna, which aids in the collection of the waves of sound, and by movement in the location of their origin. The absence of this structure in birds may be interpreted in reference to the mobility of the head and neck and to the advantage of reducing friction. The pinna is absent in aquatic mammals such as whales and seals, thus reducing friction; its muscles are vestigial in man, who has a notable power of moving his head about in trying to locate sounds. The large ear-opening lies behind and below the eye, generally well hidden by feathers, and immediately surrounded by bristles. It is very naked in ostrich and vultures. Just within the margin of the ear-opening there is often a slightly muscular fold of skin. This is represented in owls by a muscular lid in front of the opening, and doubtless corresponds rather to the ear-valve in the crocodiles than to an

ear-trumpet. That the complication should occur in owls may be associated with the nocturnal habits of these birds. Mr. Beebe suggests that the movable flap may help the owl in focussing the sounds made by mice and other small booty on the ground. In the courtship dance of the cock capercailly the ear is blocked for a brief moment at the climax of the excitement by the swelling up of an erectile fold in the outer ear-passage.

The short outer ear-passage (external auditory meatus) has stretched across it as usual the drum or tympanum, which made its first appearance in amphibians. From this taut membrane, which vibrates as the waves of sound strike it, the vibrations pass down a delicate rod or columella whose expanded inner end abuts on a window (fenestra ovalis) into the internal ear, the proper organ of hearing, which is lodged in the recesses of the periotic bone. The vibrations conveyed by the columella affect the fluid in the inner ear, and through that medium the hair-like endings of the auditory nerve.

The story of the Capitol geese is typical of many records of the quick sense of hearing in birds. This is confirmed by everyday observation, but it is noteworthy that many birds are very indifferent to loud noises, such as those of a passing locomotive or a bursting shell. As with other creatures, attention is paid to sounds which interest either inborn equipment or acquired associations. Too much must not be made of the argument that birds must have a keen sense of hearing because many of them are fine songsters, for one is reminded that many insects are very skilful instrumentalists and yet we know almost nothing in regard to the sense of hearing in insects.

Around the main chamber of the inner ear lie the three semicircular canals, in three different planes. They contain fluid and there are very numerous nerve-endings where they join the main chamber. Experiments show that they have a balancing or equilibrating function, and it is interesting to remember that this, and not hearing, is the chief use of the ear in backboneless animals. When all

the semicircular canals are injured, the bird loses all power of effective movement. When one is injured the result is a particular disability, such as falling backwards, which varies according to the particular canal that is affected. The semicircular canals are first seen in fishes, and are present in all vertebrates with normally developed ears.

According to Laudenbach (1905) there is a correspondence between the degree of development of the semicircular

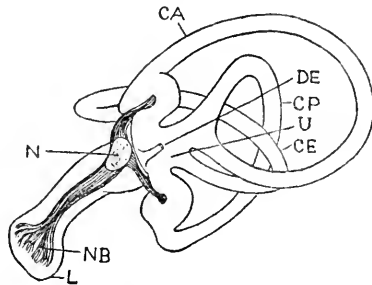


FIG. 48.—Diagram of a bird's ear. C.A., anterior semicircular canal; C.P., posterior semicircular canal; C.E., external semicircular canal; N., the cut end of the auditory nerve from the brain; three branches of the auditory nerve are shown dark; U., the utriculus of the ear into which the three semicircular canals open; D.E., the ductus endolymphaticus, rising from the sacculus, another chamber of the ear; the ductus endolymphaticus enters the brain-case and ends in the firm membrane or dura mater surrounding the brain; the sacculus also gives off a slightly bent cochlea or lagena (L.), in which are seen the ramifications of one of the branches (N.B.) of the auditory nerve.

canals and the precision of equilibration in flight. An investigation of a representative series showed that the semicircular canals were best developed in the swallow and least developed in swimming birds.

§ 3. THE OTHER SENSE-ORGANS

Sense of Smell.—Only in a few birds has the sense of smell been strictly demonstrated, *e.g.* in magpie, blackbird, owl, and night-hawks; and it may be said generally that olfactory impressions are of relatively little importance in birds, compared with mammals. What a contrast between the wide, soft, moist nostrils of most mammals,

with a large surface of olfactory membrane spread over twisted turbinal or scroll bones in the nasal chamber, and the narrow horn-encased nostrils of birds, with very little hint of turbinal bones. In some birds, like pelicans and cormorant, the nostrils of the adult are closed up. The Kiwi or Apteryx is the only bird with the nostrils at the tip of the bill; in all other birds they lie far back at the base of the bill.

It is by sight not by smell that the eagles or vultures gather to the carcass. One bird sees the dead or dying animal and descends on it, the descent of the first is seen by a second, and so the news travels from one aerial outlook to another. The nerve-endings on the olfactory membrane are contact-receptors, that is to say, odoriferous particles, either in a solid or a vaporous state, must land on the moist surface of the membrane. The fibres from the nerve-endings combine to form the olfactory nerve leading into the front of the cerebral hemispheres of the brain.

In connection with the relative unimportance of the sense of smell in most birds, it is interesting to notice that birds produce little odour. Apart from the occasional presence of small glands in the vicinity of the ear-opening, birds have only one skin-gland—the preen-gland at the root of the tail, and its secretion has little odour to us. Thus in birds recognition is mainly by sight, whereas in mammals odour helps not a little. The cleverness dogs show in detecting a bird's presence by scent shows that birds have their odours, but the point is that these are delicate and do not seem to be of much importance in the relations of birds to one another. An interesting detail which some naturalists vouch for is that the odour of some birds, *e.g.* partridge, is reduced to a minimum when the bird is brooding.

Sense of Touch.—Most of the bird's body is obviously covered with feathers, horn ensheathes the jaws, scales invest the toes, and the fingers are hidden, so that there is relatively little opportunity for the development of tactility. There are nerve-endings, however, at the base of many of the feathers, the tip of the tongue is often a touch-organ,

and many birds have a sensitive skin on their bills. This is most marked in birds that probe in the mud or soil for food, such as snipe and woodcock ; they are able by touch to detect the presence of food which they cannot see. The tactility is sometimes especially localised in a swollen white patch near the nostrils, which is called the cere because of its waxy appearance.

Sense of Taste.—Most birds eat in a hurry ; it is precarious to take time to test and chew. The sense of taste is poorly developed. Perhaps most of them are specialists in diet, keeping to one kind of food which they recognise by sight. In some cases the tongue is very horny, as in parrots, and is used to rasp the pulp of fruits from the stone ; in other cases, as in woodpeckers and humming-birds, the tongue helps to convey the food to the mouth ; in other cases, such as ducks, the tongue is a touch-organ. Only in a few cases does taste appear to be of much importance. Experiments show, however, that hungry birds will reject tempting morsels which have been dipped in some unpalatable fluid, and there are sometimes taste-papillæ on the tongue, that is to say, nerve-endings receptive to substances dissolved in the mouth.

§ 4. THE INCLINED PLANE OF ANIMAL BEHAVIOUR

Every one is agreed that the various forms of animal behaviour are on different levels of complexity, and we have tried to express this in a diagram (Fig. 49).

The theory behind the diagram is twofold : (1) that as we ascend the series of animal agencies it becomes increasingly necessary to recognise a mental or psychological aspect ; and (2) that animal activities are either predominantly reactive or predominantly initiative, either (in the main) the expression of what is hereditarily enregistered, or (in the main) the expression of new tentatives or experiments. The contrast will become clearer as we proceed.

The aim of science is to discover descriptive formulæ

which cover the facts as simply, as shortly, and as consistently as possible. When the formula "reflex action" suffices satisfactorily, there is no need to complicate matters by reference to "latent mentality," though other reasons may lead us to this postulate. At a certain level in animal behaviour we find it impossible to give an adequate description without using psychological terms, like awareness, perception, judgment; and then we are justified in speaking of, let us say, the bird's mind. What the bird's mind may be in relation to the bird's nervous system, what the bird's thinking may be in relation to the bird's metabolism, is the most difficult of all questions—probably because we have not learned to put it rightly. We are evading this question here by assuming that the psychological and the physiological, the mental and the metabolic, are correlated aspects of one reality—the life of the creature. At one time it is most prominently a body-MIND (bio-psychosis); at another time it is most prominently a mind-BODY (psycho-biosis); perhaps it is always both. At the lower end of the inclined plane the psychical aspect is often, for practical purposes, negligible. At the upper end the psychical aspect is predominant. The double lines of the diagram express this two-aspect theory.

(1) In very simple organisms we see reactions to changes in the surroundings, *e.g.* encystment when drought sets in. We also see almost explosive liberations of stores of potential chemical energy, as in the sudden protrusion of a long thread of protoplasm. Perhaps the same primitive activity may be seen in the embryonic cells of higher animals.

(2) A step higher brings us to fixed reactions, uniform answers which are given to a variety of environmental questions. They are doubtless the outcome of the selection of the relatively fitter responses. Thus the Slipper Animalcule (*Paramœcium*) reverses its cilia, backs away from an obnoxious stimulus, turns slightly on its own axis, and goes forward again. This is its fixed reaction—the answer it gives to practically every question. On the other side

we see the beginning of experiment—simple tentatives, as when an *Amœba* hunts another *Amœba*.

(3) A third level is illustrated on its reaction side by simple reflex actions, as when a sea-anemone grapples an animal that has touched its tentacles, or when an earth-worm jerks itself into its hole when the earth vibrates under the blackbird's light tread. These responses depend on inborn, pre-established linkages between certain nerve-cells and certain muscle-cells. On the experimental side may be ranked those cases where an animal, faced by some "problem," tries its repertory of reactions, one after the other, until, perhaps, it finds one which offers a solution. The Trumpet-Animalcule (*Stentor*) on which the experimenter showers microscopic dust will try three reactions before it comes to that of loosening itself and swimming away. A Brittle-star entangled in little hoops of metal over its gymnastic limbs will try a variety of movements before it gets free, but as it becomes more experienced it reduces the number of useless attempts, thus striking a new note—the beginning of *learning*.

(4, 5, 6) On a higher level must be ranked compound reflex actions, tropisms, and enregistered rhythms. When the nestling opens its mouth at the touch of the food in its mother's bill, and then proceeds to swallow, the behaviour is reflex. But the reflex actions that are involved are more complicated than those of the sea-anemone closing its tentacles.

By a tropism is meant an engrained constitutional obligation to adjust the body so that the two sides—it may be the two eyes, ears, nostrils—are equally stimulated. It is an automatic means of securing physiological equilibrium. When young eels are ascending the river they automatically adjust themselves so that both sides of the body are equally affected by the pressure of the stream. Thus they tend to swim straight up-stream. When a moth flies past a candle and has its right eye much more illumined than its left, it automatically adjusts its body so that equilibrium of stimulus is attained. Thus it often flies into the

flame. When carrier-pigeons make from a distance for their home, they may be utilising some tropism as well as the results of geographical education. When a migrant bird flies in a constant direction across the pathless sea it may be automatically obeying an engrained tropism.

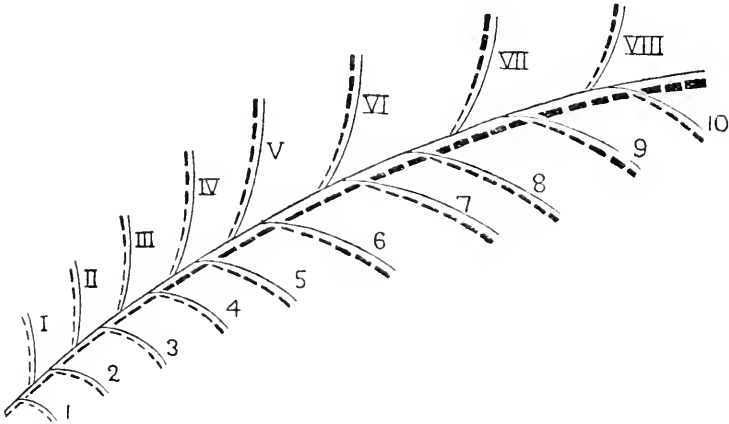


FIG. 49.—Diagram illustrating the inclined plane of animal behaviour. I., very simple actions; 1, reactions; II., simple tentatives; 2, fixed reactions; III., trial and error experiments; 3, simple reflexes; IV. V. VI., experiments, experiential learning and associative learning; 4, 5, 6, more complex reflex actions, tropisms, and enregistered rhythms; VII., intelligent behaviour; 7, 8, simple instincts and chain instincts; VIII., rational conduct (confined to man); 9, habituated intelligent behaviour; 10, unconscious cerebration. Each line is drawn double, the convex side indicating biosis or physiological processes, the concave side indicating psychosis or mental processes. As we ascend the series the psychical aspect becomes more and more obvious.

The well-known Planarian worm called *Convoluta* ascends to the surface of the sand whenever the tide goes out, and disappears below the surface whenever the tide comes in. This is more than reaction to stimuli, for the worms will manifest the same periodicity in a tideless aquarium, and will continue doing so for some time. There are many of these enregistered rhythms in the internal economy of animals. It is probable that they account in part for the restlessness of migrant birds when the time comes for their journey.

We suggest forming a group of these three kinds of behaviour—compound reflex actions, tropisms, and enregistered rhythms, because they grade into one another. And about the same area on our inclined plane we may rank non-intelligent experimenting, experiential learning, and associative learning.

A careful naturalist has described the occasional combat between a starfish and a small sea-urchin, in the course of which the starfish persists in a rather tedious process of disarming the sea-urchin, wrenching off its scissor-like snapping blades. As the starfish has no nerve-centres, not to speak of brain, it is unwarrantable to use any big psychological term. It seems to be the outcome of non-intelligent experimentation. Let us take a possibly clearer case, a starfish turned upside down. The animal rights itself after a series of movements. When the experiment is repeated day after day, the starfish *learns* (but not intelligently) to right itself more quickly, with fewer useless movements.

But there are higher grades of "learning," as when frog or tortoise becomes able to find its way quickly out of a labyrinth or maze. It learns from its experience, but how it does so remains obscure. That it discovers the secret of the maze may be ruled out, and that it forms a mental picture is also impossible. Slightly higher is associative learning, which is very common among animals. At a given signal certain fishes come to the bank for food ; when a peculiar sound is heard the dog acts in a perfectly precise way ; when a bird hears a certain voice it becomes excited. In hundreds of cases a certain stimulus comes to be associated in the individual lifetime with a particular experience or a particular course of action. Much of the education of young birds by their parents depends on the establishment of associations.

(7, 8) On a higher level on "the reaction side" are simple instincts and chain-instincts. It is characteristic of instinctive behaviour that it depends on inborn pre-arrangements of certain nerve-cells and certain muscle-cells, that it does

not require to be "learned," that it is definite and related to particular circumstances, that it is shared equally by all members of the species of the same sex, that it exhibits considerable tyranny of routine. Among birds there is much instinctive behaviour in courtship, nest-building, and brooding, in dealing with food, and in achievements of locomotion.

On the initiative side, but higher than instinctive behaviour, we must now rank intelligent behaviour, which demands inferential learning. There is some degree of perceptual inference, some "picture-logic" at least, some "putting two and two together."

The frequent repetition of an intelligent action in the lifetime of the individual leads to individual habituation—but there is no conclusive evidence that this can be entailed so as to enrich the hereditary racial equipment.

It is highly characteristic of birds that intelligence and intelligent habits may mingle with instinctive behaviour in subtle ways; as we see in the individualities of nests in difficult situations or in the utilisation of difficult food-material.

The inclined plane ends on its initiative side in rational conduct, which implies conceptual inference or experimenting with abstract ideas. So far as we know, this kind of activity is restricted to man and is only occasionally exhibited.

On the enregistration side, it may be suggested that the highest grade is that of unconscious cerebration, where a result is reached, not by controlled experimenting, nor by attending the mind thereunto, but more intuitively or instinctively—as the spontaneous outcome of racial and individual engraining. The "inspiration" may take the form of a sudden action in a crisis, of solving an arithmetical or a mathematical problem without knowing how, or of a work of art. Perhaps the nightingale's song may be an illustration.

§ 5. INSTINCTIVE BEHAVIOUR

When a nestling opens its mouth at the touch of food in its mother's bill, that is a reflex action. When rooks break the shells of river-mussels by letting them fall from a height, that is probably intelligent behaviour, involving some sort of perceptual inference. Now between these two levels there is an area of activity which we call instinctive. From the physiological side, instinctive behaviour is like a chain of complex reflex actions, each pulling the trigger of its successor; but it seems to have a psychological side as well, being suffused with some degree of awareness and being backed by conscious endeavour. No learning is necessary, as in the case of intelligent behaviour, but practice may add a touch of perfection. There is often an almost tyrannical compulsion, in which routine-efficiency defeats itself, and yet there are many instances of plasticity where the behaviour is slightly adjusted to novel circumstances. Of birds and mammals it may be said with some probability that some hitch in the instinctive routine is often an opportunity for intelligence to take the reins. But there is no warrant for regarding instinct either as "low-grade intelligence" or as "lapsed intelligence"—it is on a different evolutionary tack. While intelligence is as much made as born (though the general capacity of learning is of course part of the inheritance), instinct is much more inborn than made.

Illustrations of Instinctive Behaviour.—A young coot swims right away when it is tumbled into the water for the first time, and this is true in many cases. The capacity for executing the requisite swimming movements is laid down as part of the constitution, as a pre-established concatenation of certain nerve-cells and certain muscle-cells. But it requires an appropriate stimulation to set it agoing, and this may be supplied by some teaching on the parent's part. Thus in the case of the great crested grebe the mother plays a part in educating the young ones for

aquatic life. She takes them on her back and then sinks beneath the water, leaving them gently afloat. Among guillemots and razorbills and other members of the auk family there is often some coercion in the early training, and indeed the first plunge from the cliff into the sea would try any creature's nerve!

Our first point, then, is that many effective things that birds do are the expressions of innate predispositions of a very definite kind, which result in pecking, scratching, swimming, diving, flying, crouching, lying low and so on. But this repertory is much more limited in birds than in creatures like bees and wasps, which belong to the "little-brain" line of evolution. Professor Lloyd Morgan found that his chicks, incubated in the laboratory, paid no attention to their mother's cluck when she was brought outside the door. Although thirsty, and willing to drink from a moistened finger-tip, they did not instinctively recognise water even when they walked through a saucerful. Only when they happened to peck their toes when standing in water did they appreciate water as the stuff they wanted and raise their bills up to the sky. And was not the limited character of instinct clearly shown by the way in which they stuffed their crops with "worms" of red worsted? Evidently they were missing their mother's teaching! Limited as they were, however, they learned with prodigious rapidity, thus illustrating the deep difference between the "big brain" type, *relatively* poorly endowed with instinctive capacities, but eminently educable, and the "little brain" type, say, of ants and bees, very richly endowed with instinctive capacities but far from being quick or glad to learn. Not more than once or twice did the chicks experiment with the red worsted; not more than once or twice did they try an unpalatable caterpillar.

A good example of instinctive behaviour is seen in the obedience of many young birds to the parent's danger note. When suddenly threatened with danger the parent part-ridges utter the warning cry, and the chicks "squat flat on the ground, as if they were trying to squeeze themselves

into the very earth itself, with nothing to show the presence of life but their little black, beady eyes. As long as the danger remains imminent, the parents keep up an incessant chuck-chucking, and the chicks remain absolutely still and motionless. . . . A chick that is only two or three hours old will 'squat' at the warning cry, with the same celerity and certainty as a chick of three or four weeks. It can be no question of learning by experience and parental training. It will squat at that cry, and at that cry only, though not from any knowledge of the safety so acquired. Partridges reared under a hen never squat, although danger is threatening, and the foster-mother is clucking in a dreadful fluster. . . . The necessary stimulus is absent, and that stimulus is supplied by one particular cry of the parents and nothing else" (F. M. Ogilvie, 1920).

Intelligence Co-operating with Instinct.—Professor Lloyd Morgan reared two moorhens in isolation from their kindred, and watched them almost from hour to hour. They swam instinctively, but they would not dive, either in a large bath or in a stream, and diving is swimming with a difference. One of these moorhens, about nine weeks old, was swimming one day in a pool at the bend of a stream in Yorkshire, when a puppy came barking down the bank and made an awkward feint towards the young bird. "In a moment the moorhen dived, disappeared from view and soon partially reappeared, his head just peeping above the water beneath the overhanging bank." This was the first time the bird had dived, and yet its performance was absolutely true to type. There can be little doubt that in this case we have to recognise three factors: (1) the young moorhen had a hereditary capacity for swimming and another for diving; (2) the young moorhen had enjoyed about two months of swimming experience, which may have counted for something; but (3) the bird saw and heard the dog, was emotionally excited, and did to some extent intelligently appreciate a novel and meaningful situation. Intelligence co-operated with instinct and the young moorhen dived appropriately.

§ 6. INTELLIGENT BEHAVIOUR

When the Greek eagle lifts the Greek tortoise in its talons and lets it fall from a height so that the carapace is broken and the flesh exposed, it is making intelligent use of an expedient. Whether it discovered the expedient by experimenting, as is possible, or by chance, as is more likely, it uses it intelligently, appreciating the situation. To put it all down to the blind imitation of some original genius who discovered the device seems a violent scepticism. The same expedient is illustrated by herring gulls, which lift sea-urchins and clams in their bills and let them fall on the rocks so that the shells are broken. Rooks, which are notoriously clever birds, do the same with fresh-water mussels. There are records of a bird of prey letting food drop upon its beleaguered nestlings and of another which makes a habit of letting a stone fall into the midst of a clutch of ostrich's eggs with consequences highly satisfactory to itself.

There is much evidence that many a bird could be more intelligent if it liked to try. But given an endowment of instinctive aptitudes and a youthful schooling during which it learns with prodigious rapidity, why should a bird trouble its head with perceptual inference? To enjoy is better than to experiment, and singing a finer art than playing with syllogisms. But every now and then we hear a different note, a throb of a restless brain, the note of inquisitiveness and adventure. It implies (1) a fine brain to start with, like that of crow or parrot; (2) a certain measure of success, enabling the animal to look round with some confidence; and (3) the inducement of some probable or certain reward. Speaking of the weaver-bird (*Ploceus baya*) Mr. C. H. Donald has written (1920): "His extraordinary intelligence and his natural love for inspecting everything he sees and picking it up in his beak has been taken advantage of to teach him tricks. He is a very apt pupil, and if carefully and kindly taught will within a week select a particular

number out of many cards and bring it to his master. He will catch a two-anna piece which has been thrown into a well before it reaches the water and bring it back. Some of his tricks seem absolutely incredible, and yet one and all may be taught in a couple of days each. The first and most important step in his training is to teach him that an open hand means food and that a closed fist does not. Everything hinges on his first mastery of this secret and the rest is simple." In other words, a bird with a fine brain, which in this case had evolved for a long time in connection with the beautiful manipulation of nest-weaving, has very plastic movements and a rapid power of association.

The Hampton Court maze test has been successfully passed by the common sparrow, the cowbird and the pigeon. In the case of the pigeon the solution remained in the adult bird's possession for a month at least. Sparrows, cowbirds and chicks will also learn to discriminate clear-cut markings on cards, and a few birds have learned simple mechanisms. They usually suffer from inattention.

There can be little doubt that in the ordinary life of a young bird much depends on establishing useful associations. A moorhen chick for whom Professor Lloyd Morgan dug up worms with a spade would soon run to him from some distance when he took the spade in hand. Not from any intelligent appreciation of the spade as a digging instrument, but probably because the spade was an element in the mental registration of a pleasant experience.

The general impression that one gets in regard to the cleverness of birds in such activities as nest-building, capturing booty and dealing with food is that on an instinctive basis, varying in definiteness, there is built up a superstructure partly due to early education and subsequent imitation, and partly due to an intelligent appreciation of the lessons of experience. The difficulty is to say how much is due to the inherited "nature" (the racial legacy of wits or talents) and how much is due to individual "nurture," including in that term not only direct education on the parents' part, but personal experience as well. To decide

as to the relative importance of "nature" and "nurture" requires careful observation and experiment.

Some young woodpeckers show notable expertness in opening fir cones to get at the seeds. This might be referred to a special instinctive capacity, like that which enables the young coot to swim when it first tumbles into water. Or it might be referred to sheer cleverness, such as the inquisitively experimental weaver-birds illustrate. Yet neither interpretation is quite correct. For we have to recognise that the parent woodpeckers bring their young ones first the seeds themselves, then partly opened cones, and finally intact ones. Thus, as Professor L. T. Hobhouse says in his "Mind in Evolution" (1915), "the method of preparing the family dinner is at least as much a tradition as an instinct." It is an outcome of teaching and learning.

We cannot leave the bird's mind without referring to the well-known cleverness of rooks and parrots, and raising the interesting question how far this is due to their social life and their habit of talking a good deal. Both rooks and parrots have finely developed brains, and it was probably this possession, shared by non-gregarious relatives (such as many crows), that led to their sociality. But these things often work round in circles. Given fine brains, sociality and loquacity may follow; but sociality and the possibility of some talking together form appropriate sieves for the sifting out and retention of progressive variations in the direction of nimbler wits. A great law of evolution is that to him that hath more shall be given.

Behind and beneath the modes of behaviour—whether instinctive or intelligent or both—there are the primary appetencies of "hunger" and "love." They have their physiological aspects—the bodily "urges" which demand satisfaction; but they have also their psychological aspects—the longings and desires of the subjective life. Exaggerations of the one aspect lead us to make too much of the empty stomach and the tumescent reproductive organs. Exaggerations of the other aspect lead us to make too much of "the self-preservative instinct" and the "love" of

mates. The probable truth is that these are the two sides of one shield, and that particular types and exaggerated individuals are sometimes predominantly mind-*bodies*, while others vindicate their right to be regarded as likewise body-*minds*.

Finally, it must be recognised that the mentality of birds includes a wealth of feeling, rising in these highly strung creatures to genuine emotion.

CHAPTER XIII

THE PEDIGREE OF BIRDS

- § 1. The Oldest Known Bird. § 2. Affiliation of Birds to Reptiles.
§ 3. Resemblances in the Development of Birds and Reptiles.
§ 4. From which Reptilian Stock? § 5. Speculations. § 6. Primitive Toothed Birds. § 7. Running Birds. § 8. Flying Birds.
§ 9. The Process of Evolution.

§ 1. THE OLDEST KNOWN BIRD

THE first remains of an undoubted bird are those of Archæopteryx in the lithographic stone strata of Bavaria, which are referred to the Jurassic age. Two fine specimens are known, and these show certain reptilian affinities—an indication of the affiliation of birds to some reptilian stock. The following may be mentioned: teeth in both jaws (three visible above and thirteen below); a long tail like a lizard's with about twenty vertebræ; a set of "abdominal ribs"—subcutaneous ossifications running across the ventral surface of the abdomen—similar in a general way to those in the crocodile and some other reptiles; three clawed fingers and the palm or metacarpal bones separate from one another—a sort of half-made wing in short. Yet the bird-like characters of Archæopteryx are plain enough, *e.g.* the feathers which have left their imprint on the fine-grained stone, and the general nature of skull, hip-girdle, and hind legs. It was about the size of a crow.

Although Archæopteryx is much too specialised to be regarded as the first bird, it seems fair to say that it was a primitive bird with some striking reptilian features. There are other extinct birds with indubitably primitive characters,

such as *Hesperornis* and *Ichthyornis*, both with a good equipment of teeth, but apart from teeth there is not much more of the reptile in them than we can find in any ordinary bird.

The rock record shows that there was a time when the highest backboned animals on the earth were Reptiles ; and

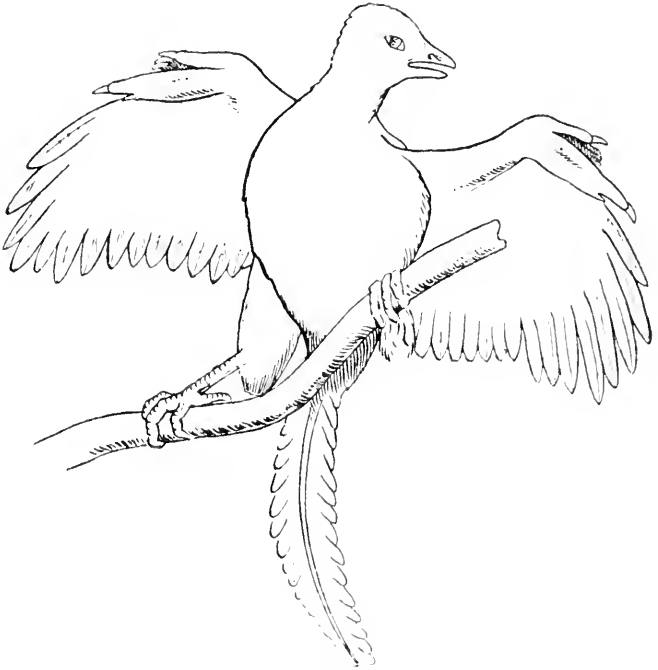


FIG. 50.—Restoration of *Archæopteryx*.
(By kind permission of Mr. W. P. Pycraft.)

the cumulative evidence in support of the evolution-idea leads one naturally to think of Birds (and Mammals too) as arising from some reptilian stock. Yet the antithesis between flying birds, the creatures of the air, and grovelling reptiles, the creatures of the earth, is so striking that it is only reasonable to inquire into the evidence, apart from the connecting link of *Archæopteryx*, in support of the conclusion.

§ 2. AFFILIATION OF BIRDS TO REPTILES

A bird is known by its feathers, and no transition is known between feathers and any other integumentary structure, yet we have only to look at the tarsometatarsus (ankle-and- instep region) of an ordinary bird to see that the legacy of reptilian scales is not lost. There is no doubt, moreover, that the horny covering of a bird's beak is comparable to the scales of reptiles, especially when we notice that in old-fashioned birds like the albatross and the petrel it is compound, that is to say built up of many separate pieces. An interesting corroboration is to be found in the fact that the puffin moults the outer covering of its bill-scales every year, a process much nearer to the moulting seen in reptiles (where the outer layer of the epidermis covering the scales is peeled off) than to the moulting seen in birds (where individual feathers fall off as such). Another hint of affinity may perhaps be found in the little hardening of horn and lime formed at the tip of the bill of many birds before they are hatched, and somewhat unfortunately called the egg-tooth. For a similar structure, apparently of use in breaking out of the egg-shell, is found in some unhatched reptiles. It appears in birds even before the laying down of the horny bill, and the suggestion has been made that it is the last relic of a very ancient armature, older than ordinary scales.

There is often a claw on the thumb of a bird's wing, and sometimes, as in the ostrich, on the first finger as well. In the young Hoatzin (*Opisthocomus*) the claws on the thumbs are unusually long, and are mobile enough to be used in scrambling. In *Archæopteryx* there was a claw on each of the three digits. Here again, therefore, there are relics of reptilian ancestry.

The skull of a bird is very different from that of any reptile, and yet the two types agree in having one occipital condyle for working against the first vertebra, a complex mandible or lower jaw made up of 4-6 bones on each side, an articulation of the lower jaw with the quadrate in the

posterior part of the skull, and a delicate rod of bone (the columella) passing from the drum or tympanum to the inner ear. All of these are characters of some importance, indicative of genuine affinity. And the point becomes clearer when it is noted that not one of these features, common to birds and reptiles, is to be seen in mammals. For in mammals there are two occipital condyles, the mandible is one bone on each side, it articulates with the squamosal, the quadrate has probably become one of the three ear-ossicles (the incus), and the place of the columella is probably taken by another ear-ossicle—the stapes.

In some other regions of the body, both in hard and soft parts, affinities with reptiles can be detected, but it may be enough to give two other instances. When a reptile moves its ankle-joint, it is working the upper or proximal row of tarsal bones against the lower or distal row. This is called an *inter-tarsal* type of ankle-joint, in contrast to what is found in mammals (*cruro-tarsal*), where the lower end of the tibia works against the astragalus, and the lower end of the fibula, it may be, against the os calcis. (The astragalus and os calcis form the two tarsal or ankle bones of the upper or proximal row.) Now in birds there are no ankle-bones left in the fully-formed skeleton, and yet the ankle-joint is *inter-tarsal* as in reptiles. For the proximal tarsals fuse to the lower end of the tibia and the distal tarsals fuse to the fused metatarsals, the plane of ankle-movement remaining between the two rows of tarsals, though the bones as such have disappeared. This is the kind of exception that proves the rule.

As regards soft parts, it should be recalled that the crocodilians have a four-chambered heart as birds have, though they do not make so much of it; that the blood is much the same in bird and reptile; that air-sacs, so characteristic of birds, are seen in the chamæleon among lizards; and that the urogenital system of birds is plainly derivable from the reptilian type.

§ 3. RESEMBLANCES IN THE DEVELOPMENT OF BIRDS AND REPTILES

Birds and reptiles have the same type of egg, the true ovum or egg-cell becoming enormously dilated with yolk and surrounded by albumen and a shell. The egg of a crocodile is like the egg of a goose, both externally and internally. On the top of the yolk, in both cases, there lies a drop of living-matter with a nucleus, and this segments after fertilisation into a disc of cells or blastoderm. In other words, there is in birds and reptiles a process of partial discoidal segmentation. The early embryonic stages are closely alike. In both, for instance, there appears along the dorsal median line a "primitive streak," and soon afterwards in the same line a primitive groove—the beginning of the establishment of the nervous system. In both, again, there appear at an early date two fœtal membranes—the protective amnion and the respiratory, excretory, and nutritive allantois. The unhatched bird and the unhatched reptile breathe in the same way, for the oxygen that finds its way through the shell is absorbed by the blood-vessels of the allantois spread out underneath. In short, the early development of the bird closely resembles the early development of the reptile. For days they travel, as it were, side by side along the same broad highway, and it is only gradually that they diverge along avian and reptilian paths. In the case of the chick it is not till the sixth day that definitely "avian" characters begin to appear.

It is often from relatively unimportant details that the most convincing evidence comes. Thus in the embryo of the very old-fashioned South American Hoatzin (*Opisthocomus*) there is a paw-like hand with three clawed fingers, and there are numerous elements in the wrist. It was this sort of evidence that led W. K. Parker, one of the early students of the embryology of the bird's skeleton, to declare that the bird is "a transformed and, one might even say, a glorified reptile."

§ 4. FROM WHICH REPTILIAN STOCK ?

The threefold evidence (*a*) from anatomical resemblances, (*b*) from similarities in early development, and (*c*) from Archæopteryx as the oldest avian type, points unhesitatingly to the conclusion that Birds evolved from a Reptilian stock. The question is from which ?

From Pterodactyls ?—It is natural to think first of the extinct “flying dragons,” the Pterodactyls or Pterosaurs, as a possible ancestral stock. They could to some extent fly; they had long bones of the hollow girder type, so characteristic of birds; there is a fusion of dorsal vertebræ as in flying birds; and some of them show a slight keel on the breast bone. But most of the resemblances may be easily interpreted as convergences, that is to say, as similar adaptations to similar habits and conditions of life. They are negatived by dissimilarities in many parts of the skeleton, such as the hip-girdle and the vertebral column, and by the obvious difference in the whole nature of the wing. For the Pterodactyl’s wing is a patagium-wing, with a web of skin spread out on an enormously elongated outermost finger, and continued back to the hind legs and the tail, while the Bird’s wing is a feather-wing—an altogether different idea. The Pterodactyl’s wing is as different from a Bird’s as a Bat’s is.

From Dinosaurs ?—There is more to be said for seeking the origin of birds in a Dinosaur stock—an extinct order or class of terrestrial Reptiles with great diversity of habit. Some were quadrupeds, others were at times or habitually bipedal. In the sub-division known as the Ornithischia the hip-girdle closely approaches the bird type, and there is also a tendency to form a tarso-metatarsus. It has to be admitted, indeed, that no Dinosaur shows any approach to the bird’s wing, but, as we indicated in our first chapter, it is not unreasonable to suppose that birds had got well under weigh as running and jumping bipeds before feathers appeared and the transformation of a fore-limb into a wing

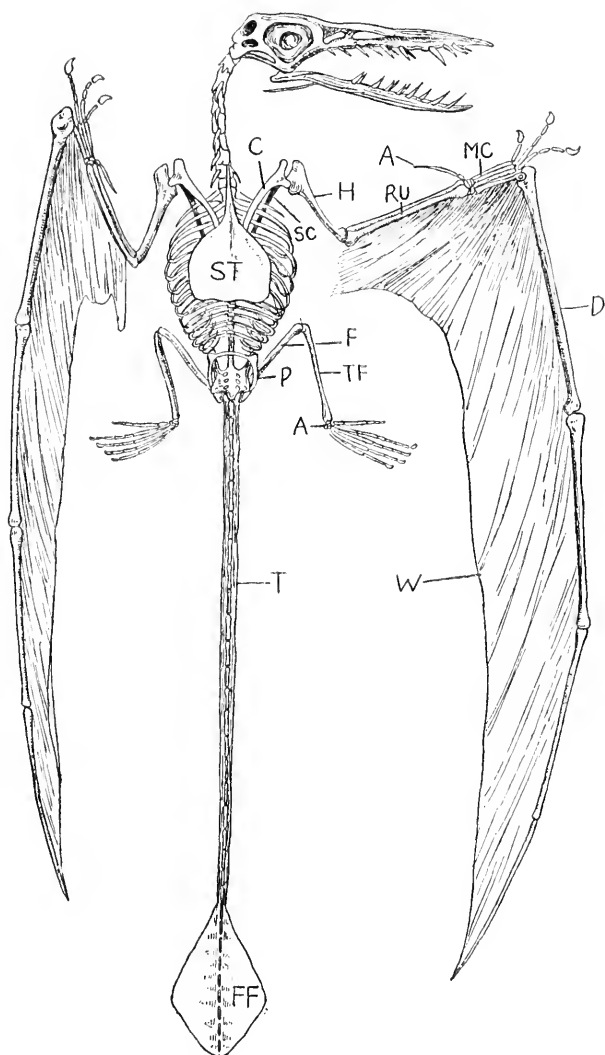


FIG. 51.—Skeleton of a Pterodactyl. ST., breastbone; T., tail; FF., terminal flap; W., wing; D., greatly elongated outermost finger; MC., metacarpals; RU., radius and ulna; H., humerus; SC., scapula; C., coracoid; P., pelvic girdle; F., femur; TF., tibia and fibula; A., ankle bones. The A. on the wing is an extra bone arising from the wrist.

began. It seems quite safe to say that birds evolved from a reptilian stock ; it seems reasonable to regard Ornithischian Dinosaurs as not far off the pedigree of birds ; but beyond these general statements very little can be said with security. As is usual in regard to " big lifts " in organic evolution, we must frankly admit ignorance. We must, however, hold firmly to the general idea, as Professor W. K. Parker expressed it, that birds began as " fevered representatives of reptiles, progressing in the direction of greater and greater constitutional activity."

§ 5. SPECULATIONS

(1) Some authorities, such as the Hungarian palæontologist Nopcsa, have suggested that birds arose from long-tailed, bipedal reptiles, which ran and leaped along the ground, flapping their fore-limbs—broadened out posteriorly, first by scales and eventually by feathers.

(2) Other authorities, such as Osborn, have suggested that birds arose from arboreal reptiles, which were in the habit of parachuting or volplaning from tree to tree. As feathers evolved and the breast muscles strengthened, the more or less passive parachute became an active wing which could be used to strike the air. This view receives support from the analogy of bats, for it is practically certain that they evolved from Insectivora, among which the aberrant Galeopithecus shows a finely developed patagium or parachute.

(c) Beebe has made the interesting suggestion that birds passed through a " four-winged or Tetrapteryx " arboreal stage when the legs bore backward-directed feathers like those on the arms, both sets serving as parachutes for gliding. There seem to be indications of tufts of feathers on the hind limb of Archæopteryx and of sprouting quills in the same position on some newly hatched birds.

(d) Dr. W. K. Gregory (1916) suggests a sort of compromise, and we must keep in mind the possibility that birds had a *dual* origin, some from cursorial and others from arboreal ancestors. " The pro-Aves were surely quick

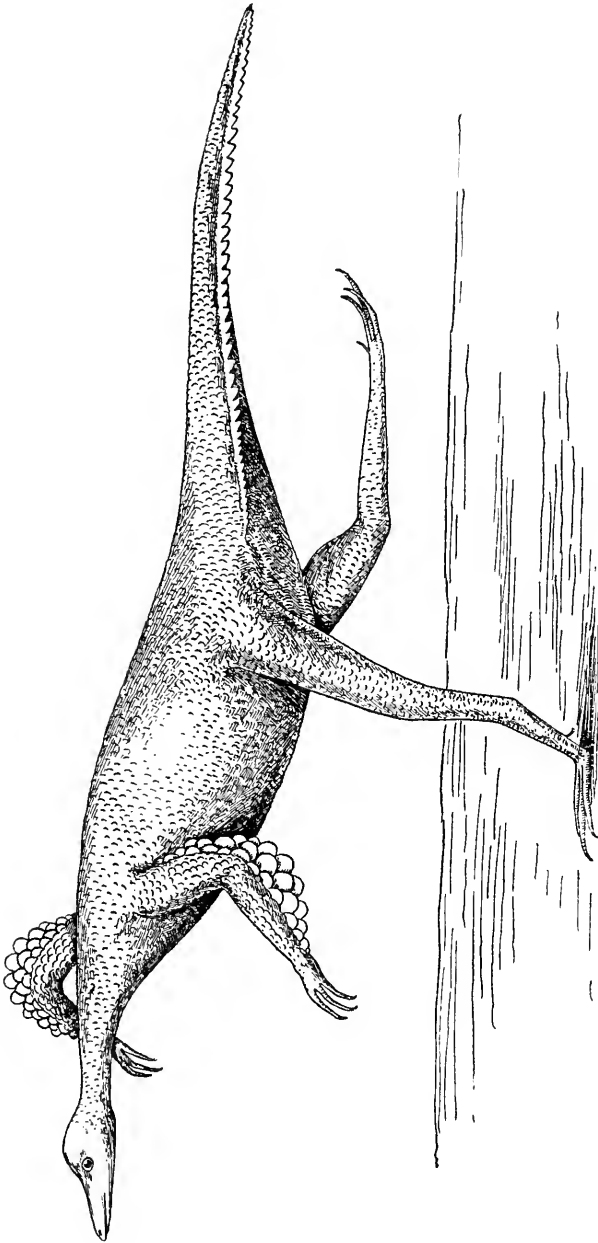


FIG. 52.—Nopcsa's idea of an ancestor of birds,—a long-tailed, bipedal reptile, with broad scales on the posterior margins of the arms, which it flapped as it ran.

runners, both on the ground and in the trees, but it is not yet clear whether the upright position was first attained upon the ground or in the trees. They very early acquired the habit of perching upright on the branches, as shown by the consolidated instep bones, grasping first digit, and strong claws of *Archæopteryx*. Their slender arms ended in three long fingers provided with large claws which were at first doubtless used in climbing.

“These active pro-Aves contrasted widely in habits with their sluggish remote reptilian forebears. In pursuit of their prey they jumped lightly from branch to branch and finally from tree to tree, partly sustained by the folds of skin on the arms and legs, and later by the long scale-feathers of the pectoral and pelvic ‘wings’ and tail. That they held the arms perfectly still throughout the gliding leap still appears doubtful, for no recent animals that do that have attained true flight. I cannot avoid the impression that a vigorous downward flap of the arms, even before they became efficient wings, would assist in the ‘take-off’ for the leap, and that another flap just before landing would check the speed and assist in landing.”

As already indicated, the speculation that most commends itself to us is that birds began as runners and jumpers, that they secondly passed through an arboreal apprenticeship of climbing and volplaning, and that they finally became able to strike the air with wings on which the patagium, still persisting in part, gradually gave place to pinions.

§ 6. PRIMITIVE TOOTHED BIRDS

Archæopteryx flourished in Jurassic times; in the next geological period, the Cretaceous, there were primitive toothed birds, the *Odontolcæ*, probably an offshoot from the main Avian stem. The Upper Cretaceous rocks of Kansas have yielded good skeletons of *Hesperornis regalis*, a flightless aquatic bird, probably related to the modern grebes and divers (*Colymbidæ*). It was about a yard high; it had rudimentary wings and no keel on the breastbone; it had

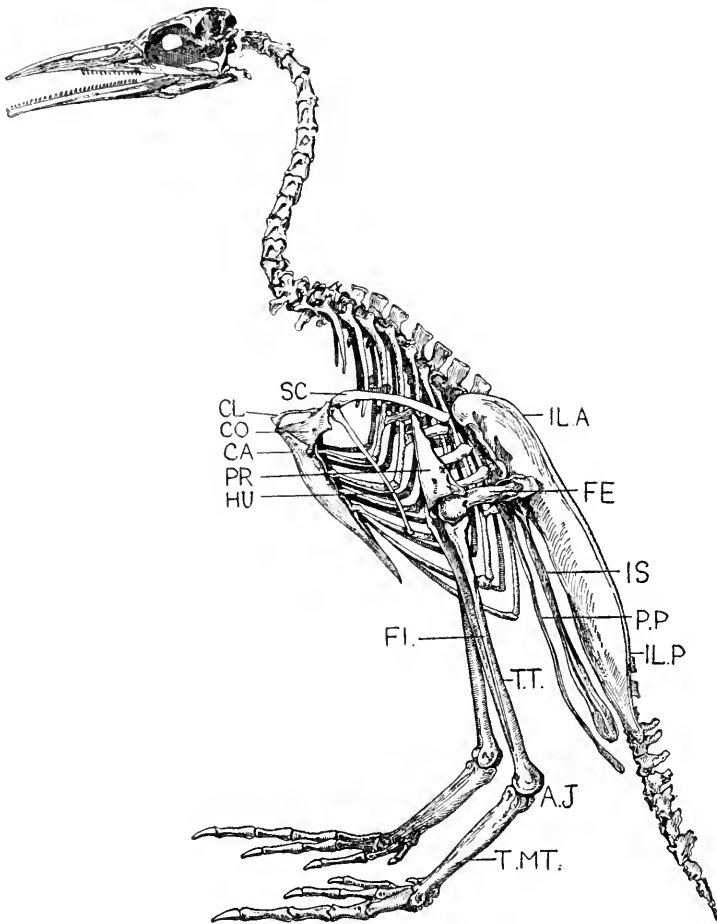


FIG. 53.— Skeleton of extinct *Hesperornis*. After Marsh. SC., scapula; CL., clavicle; CO., coracoid; CA., carina or keel; HU., reduced humerus; IL.A., anterior end of ilium; IL.P., posterior end of ilium; IS., ischium; P.P., post-pubis; FE., femur; PR., knee process; FI., fibula; T.T., tibio-tarsus; A.J., ankle-joint; T.MT., tarso-metatarsus.

powerful hind legs well suited for energetic swimming. There were teeth in grooves in both jaws. A British ally has received the name of *Enaliornis*. They probably represent, as Dr. A. Smith Woodward says, "an early specialised offshoot from the common ancestral type of the two great surviving orders," namely, the Running Birds and the Flying Birds.

About the same time that *Hesperornis* swam about in Cretaceous seas, like a gigantic loon, there was another toothed bird, *Ichthyornis victor*, much smaller (towards a foot high) but hardly less remarkable. It was a delicately built creature, with well-developed wings and a strong keel. The teeth were in distinct sockets and the vertebræ were biconcave—two very striking features, harking back to reptiles. But it was far away from *Hesperornis*, and was definitely on the modern bird tack. Of its affinities, Mr. W. P. Pycraft says cautiously, "*Ichthyornis* may perhaps be, and generally is, regarded as the ancestral type of the present *Steganopodes*—the gannets, cormorants, pelicans, tropic and frigate birds."

It is interesting that in Cretaceous times there should have been living these two very different types—*Hesperornis*, a specialised aquatic bird on a line pointing to divers, and *Ichthyornis*, a flying bird, on a line pointing to solan geese. There must have been many other types, some of them connecting back to *Archæopteryx*, but the important fact is that the modern bird type had definitely emerged.

§ 7. RUNNING BIRDS

The flightless Running Birds or *Ratitæ* of to-day represent only five genera—the African Ostrich (*Struthio*), the South American Ostrich (*Rhea*), the Australasian Emu (*Dromæus*), the Austro-Malayan Cassowary (*Casuarus*), and the Kiwi (*Apteryx*) of New Zealand. To these, according to some authorities, the Tinamous should be added. The persistence of the *Rhea* and of the Kiwi is seriously threatened, and the comparatively recent extermination of

the Moa (*Dinornis*) of New Zealand suggests that terrestrial flightless birds express a dangerous contradiction in terms. The giant *Æpyornis* of Madagascar disappeared long ago.

There are two views of Running Birds. (a) On one view, they are primitive, old-fashioned forms, which never had flying wings nor a keel on their breastbone. (b) On the other view, they are creatures that have gone back and have become secondarily wingless. Thus Professor W. K. Parker spoke of them as "overgrown, degenerate birds that

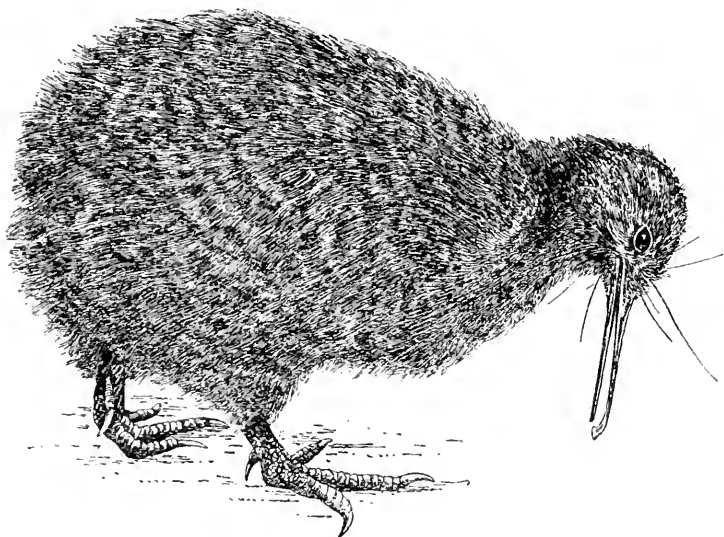


FIG. 54.—The Kiwi or *Apteryx* of New Zealand, with quite rudimentary wings.

were once on the right road for becoming flying fowl, but, through greediness or idleness, never reached the 'goal'—went back, indeed, and lost their sternal keel, and almost lost their unexercised wings."

(a) In support of the view that the *Ratitæ* represent a somewhat primitive stock that never attained to flight, it may be noticed that they betray a certain old-fashionedness in some of their features. Thus there are no regularly arranged feather-tracts or pteryllæ, there is no ploughshare-

bone at the end of the tail, the hook-like (uncinate) processes on the ribs are small or absent, the barbs of the feathers do not form a coherent vane, and the sutures of the skull-bones remain for a long time distinct, whereas in Flying Birds they almost always disappear very early.

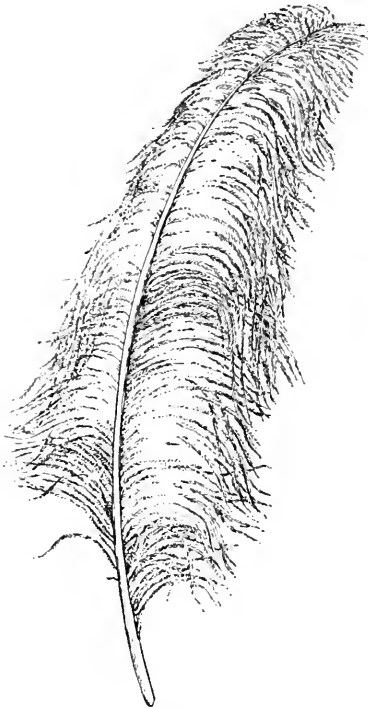


FIG. 55.—An ostrich feather, the barbs free from one another, not forming a vane.

(b) In support of the view that Running Birds are degenerate Flying Birds, a strong argument is furnished by the Tinamous or Crypturi, partridge-like birds of Mexico and Central and South America. They are great runners, but they have also strong and rapid flight. The breastbone bears a keel, and yet in the skull and in some other skeletal features there is a marked resemblance to ostriches and their relatives. For the Ratitæ differ from all other birds except Tinamous in the nature of their palate: the pterygoids form a jointed articulation with the palatines, and a close union either

by fusion or by overlapping suture with the base of the well-developed vomer. This kind of skull, called dromæognathous, is very distinctive. Tinamous are often ranked with Carinatae because they are flying birds with a keel, but their skull is distinctly struthious. This suggests that the struthious Running Birds may have degenerated from flying birds somewhat like Tinamous. The disappearance

of the keel on the breastbone presents no difficulty, for it has disappeared in various "Carinate" birds, such as the burrowing parrot called Stringops. Of course the argument

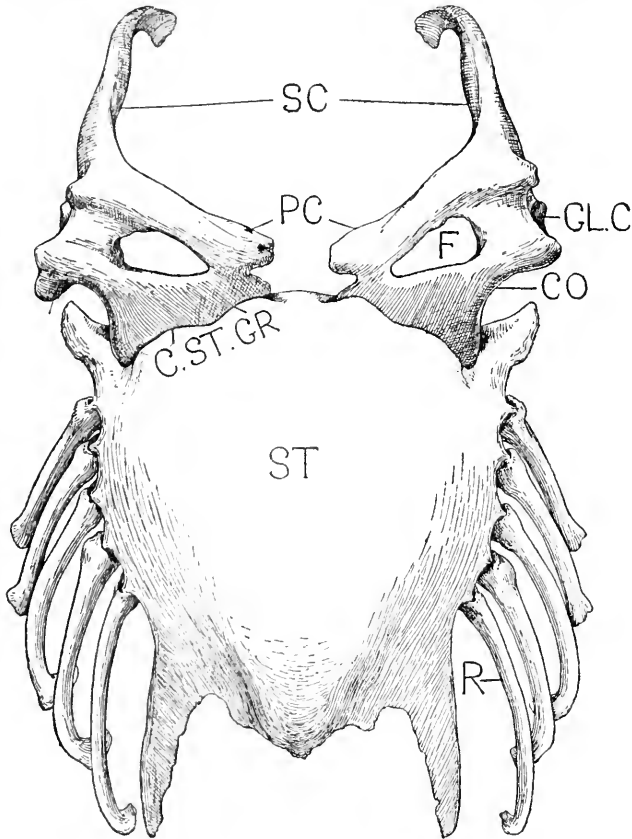


FIG. 56.—Pectoral girdle and breastbone of an ostrich (*Struthio*). sc., scapula; co., coracoid; pc., precoracoid; f., foramen; gl.c., the glenoid cavity with which the humerus articulates; c.st.gr., the coraco-sternal groove; st., the sternum or breastbone, without a keel, but convex outwards; r., sternal portions of the ribs. From a specimen.

is not conclusive. It is possible that the Tinamous are not *Ratitæ*, but very peculiar *Carinatæ* which sprang from a primitive stock with dromæognathous palate and distant affinities with the flightless *Ratitæ*.

Two other points may be noted. It must not be supposed that the important difference between the struthious "Palæognathine" palate and the carinate "Neognathine" palate necessarily indicates a dual origin of Ratitæ and Carinatæ. Mr. Pycraft's studies of the development of the palate show that the Neognathine palate is derivable from the other. But there is another consideration, which shows how difficult and uncertain all these discussions are, namely the question whether the Running-Birds form a coherent "order," or whether they may not represent an assemblage of forms of diverse origin which "went back" at an early stage in the evolution of birds when the palate was still at the palæognathine grade.

§ 8. FLYING BIRDS

According to Mr. Pycraft, the birds with a neognathine palate split up early into two branches, each of which divided again, so that four legions may be recognised:—

A. Colymbomorphs: Penguins, Grebes, Divers, Petrels.

B. Pelargomorphs: Storks, Herons, Anserine birds, Falcons, etc.; Pelicans, Gannets, Cormorants, etc. (Steganopods).

C. Alectomorphs: Gallinaceous birds—the Fowl tribe,—Rails, Cranes, Plovers, Gulls, Auks, Pigeons, Sand-Grouse.

D. Coraciomorphs: Cuckoos, Parrots, Hoopoes, Horn-bills, Woodpeckers, Barbets; Rollers, Bee-Eaters, Kingfishers; Owls, Swifts, Humming-birds, Mouse-birds; and the great host of perching birds or Passeres.

§ 9. THE PROCESS OF EVOLUTION

It is useful to ask at this point whether any general idea can be formed as to what has taken place in the establishment of 10,000 or more different species of Flying Birds?

We must think of each type as having an equipment of hereditary items or factors, corresponding to characters in the full-grown birds. These hereditary factors are like

cards that are shuffled at the beginning of each individual life, so that changes occur in the "hand" which each individual holds. These changes begin in the germ-cells; they find expression in development; and they are tested in the individual experience. They begin in the germ-cells as the outcome of the opportunities for permutations and combinations of factors that occur in maturation and fertilisation; they may also be incited by deeply-saturating variational stimuli which are traceable to peculiarities in the nutrition, environment, and functioning of the parent; or they may be due to subtle changes, *e.g.* growth-changes and active re-organisations, in the living germ-cells. This remains highly speculative.

It is probable that in each type, say a stork type, there is a considerable *bloc* of hereditary characters, perhaps registered in the cytoplasm of the egg-cell, in which there is little change from generation to generation. It is also probable that the germinal variations that occur are within a limited range, that they have to be congruent with what has been already securely established. It is certain that no variation can take root unless it is consistent with stability of architecture and constitution. This is prevented by the conditions of development and also by the winnowing action of Natural Selection.

Within certain limits, then, of morphogenic stability and bionomic success new departures are of unceasing occurrence, and these have formed the basis of new species. The individual gets a new hand of hereditary cards, and if it plays them well it may find some niche of opportunity which ensures success either for itself or for the progeny.

What is particularly interesting in a general survey of bird evolution is the recurrence of similar adaptations along lines which have only a distant genetic affinity. In other words, what is called convergence, the occurrence of similar adaptations in unrelated types, is abundantly illustrated in the evolution of birds.

Success in the struggle for existence depends on many factors, such as vigour and parental care, catholicity of

appetite and kin-sympathy, efficiency in using weapons and effacement by camouflage. But, in more general terms, considered in its time-relations, it depends on plasticity and an ability to seize opportunities. There must be novelties—the cards to play, and there must be ability to play them well. Birds show that nothing succeeds like success. For their independence of geographical restrictions and their individual freedom of movement give them unusual opportunities for discovering new homes, new corners, new kinds of food, new devices—and they have risen to the occasion.

CHAPTER XIV

BIRDS AND EVOLUTION

§ 1. The Fact of Evolution. § 2. Factors in Evolution. § 3. Originative Factors. § 4. Illustrations of Variations. § 5. Possible Origins of Variations. § 6. Modifications in Birds. § 7. Modificational Specific Characters. § 8. Directive Factors: Processes of Selection. § 9. Isolation and the Reverse: In-breeding and Out-breeding. § 10. Birds and Heredity.

§ 1. THE FACT OF EVOLUTION

It is the almost unanimous conclusion of modern naturalists that Birds sprang from some extinct stock of Reptiles, probably from the Ornithischian Dinosaurs. There are such very striking contrasts between the reptiles, so characteristically bound to the earth, and the birds which have achieved the mastery of the air, that the derivation of the latter from the former seems at first sight startling. We venture, therefore, to reinforce what has been said in the preceding chapter. What are the main lines of evidence?

(a) **Morphological.**—The bird betrays its reptilian origin in many a corner of its body, from the epidermic scales on its bill to those on its feet, from the complex lower jaw working on the quadrate to the inter-tarsal ankle-joint, from the sclerotic ring of bone round the front of the eye to the egg-tooth with which the chick breaks its way through the egg-shell. For all reptiles show epidermic scales and a complex lower jaw working on a quadrate; all that have hind-legs show an inter-tarsal ankle-joint; and some of them show a sclerotic ring and an egg-tooth. Unless the processes of Nature are magical, the possession of *many* structural features in common, for we have given only a few instances, must mean genetic affiliation; and the rock record shows that Reptiles appeared before Birds.

(b) **Embryological.**—The egg of a crocodile, as we have mentioned, is superficially like that of a goose and the internal structure (with the white of egg and the yolk) is the same. The early stages in development—the establishment of three germinal layers, the nervous system, the notochord, the primitive gut, the musculature, the body-cavity, and so on, take place in the same way, and it is not till some days have passed that the embryos of the reptile and the bird becomes obviously different. The similarities in the early stages of development prove genetic affiliation.

There are many features in the development of birds which point to a pedigree stretching into the obscure past far beyond the ancestral reptiles. Thus on the side of the neck of the embryo chick there are gill-clefts, opening out from the pharynx. They have no respiratory significance; indeed they have no use at all except that the first becomes the Eustachian tube from the ear passage to the back of the mouth. But they persist in every embryo bird, tell-tale evidences of a remote aquatic ancestry.

A very interesting point in regard to the embryonic gill-clefts has been demonstrated by Edward A. Boyden (1918). Across the ventral surface of the neck in the embryo chick and in some reptiles there is a band of tissue, which is derived from the ventral union of the hyoid arches. From its resemblance to the development of the gill-cover of certain fishes and amphibians it may be justly called the opercular or gill-cover fold. Now on the lateral margins of this operculum, after it has grown backward to enclose at least a potential gill-chamber, filamentous outgrowths are observed on the under side. In reptiles they have a very transitory existence, but in the chick they have a relatively extensive and prolonged development. The filamentous character of these outgrowths, their origin from gill-arches, and their relation to the operculum point to the conclusion that they are vestigial gill-filaments like those of fishes. The persistence of gill-clefts in the embryo has been for a long time familiar, but here we have a demonstration of vestigial gill-filaments as high up the scale as birds.

(c) **Historical.**—Not much can be made of the fact that some extinct reptiles could in some measure fly ; there is more importance in the fact that some of them were bipeds. The reason why no stress is laid on the flying Pterodactyls is that their wing was of a quite different type from the bird's wing. There is satisfactory historical evidence, however, in the oldest known bird, Archæopteryx, for it had several reptilian features, such as teeth, a long tail, a half-made wing with claws on three digits, and abdominal ribs. There are some other reptilian features in some other extinct birds which are not so ancient as Archæopteryx.

Let us take another little point—a straw that shows how the wind has blown. Duerden (1919) points out that at a certain stage in its development the two-toed ostrich (*Struthio*) has three toes and hints of another or of other two. That is to say, two or three toes have been lost, but the loss is not quite complete. This embryonic persistence is unintelligible except on the evolutionary interpretation that the two-toed ostrich is descended from ancestors with four or five.

§ 2. FACTORS IN EVOLUTION

Accepting the fact of evolution, what can we say in regard to the factors that may have operated in bringing it about ? Our knowledge of these factors remains very imperfect, and we are in great part restricted to an argument from analogy. We are forced in the main to argue from what goes on in the present to what may have gone on in the dim and distant past. There may be factors in evolution which have not yet been discovered, and there are possible factors (*e.g.* the transmission of acquired characters or bodily modifications) in regard to which we are in doubt. It seems useful to distinguish the *originative* factors which bring about new departures or variations, and the *directive* factors which sift or prune this material. Besides these two sets of factors there is heredity or the relation between successive generations, which determines whether a novelty will or will not be entailed on the next generation. Let us begin with the originative factors.

§ 3. ORIGINATIVE FACTORS

The general evolution idea is borne out by the occurrence of variations in birds, both in a wild state and under domestication. There are over two hundred well-marked breeds of domestic pigeons, and some ornithologists say that there are at least ten of them which would be ranked as distinct genera if they occurred wild. Yet there is very strong evidence that all are scions of the blue rock-dove, *Columba livia*, which still frequents shore-cliffs in several parts of Britain. We may go further and say that domestic pigeons evolved under man's superintendence from the particular variety of *Columba livia* which has two dark bars on its wing.

In the same way there is very strong evidence that all the breeds of poultry—Hamburghs and Dorkings, Bantams and Silkies, and all the rest of them, are descended from the jungle-fowl, *Gallus bankiva*, still found wild in some parts of India and the Malay Islands. Professor Bateson points out (1913, p. 90) that in *Gallus bankiva* there is no factor for rose comb, pea comb, barring on the feathers, or for the various dominant types of dark plumage. He thinks it improbable that the jungle-fowl could be the ancestor of some of the modern heavy breeds of poultry. But even if his suggestion be correct that some other wild *Gallus*, now extinct, took part in the genetic history of domestic poultry, it would not affect the general evolutionary fact that the diverse domestic breeds have arisen from one or more wild ancestral species.

Thus we have the general argument which Darwin elaborated in his "Variation of Animals and Plants under Domestication" (1868): If Man has been instrumental in sifting out and fixing all these varieties, say of pigeons and poultry, in a short time, what may not Nature have effected in a very long time?

Some of the varieties that have been established are so very extraordinary that one cannot help marvelling that they persist at all, even under man's ægis. In an anatomical study of the hooded fowls of the Houdan breed, Fr. Neumann

(1914) analyses some of the peculiarities. The cerebrum is greatly enlarged in front, and this may be further increased

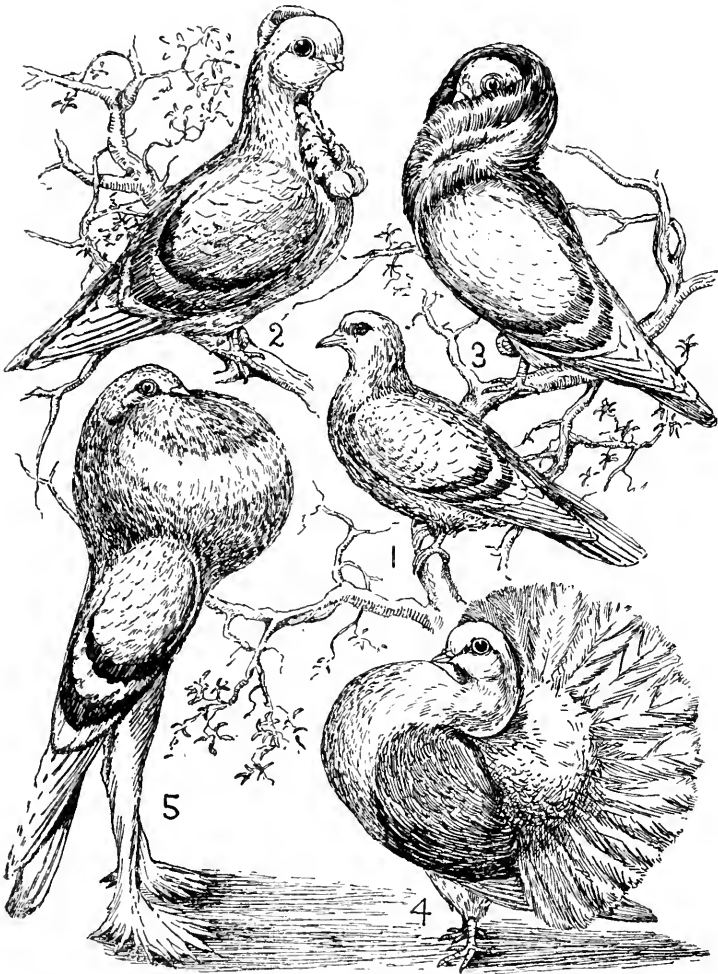


FIG. 57.—1, the ancestral rock-dove, *Columba livia*; 2, turbit; 3, jacobin; 4, fantail; 5, pouter.

by hydrocephalus. But the posterior part of the cerebrum is poorly developed, and this results in the formation of a sort of neck which slightly separates off the cerebrum from

the rest of the brain. The skull is transformed in correlation with the change in the shape of the brain ; it is raised up in the region of the frontal bones. Above this is the large tuft of head feathers, and in connection with this hood the blood-vessels of the head are quite peculiar. The comb is much reduced in the hens, less so in the cocks ; below the comb there are sometimes large vesicles containing serous fluid. All the Houdans have five toes. In short, they are bundles of abnormalities and they do not look happy after a shower of rain. But the marvel is that under man's protection the Houdans fare not badly and have persisted for many years.

There seem to be conservative as well as variable types, as may be illustrated by contrasting ostrich with pigeons or poultry. Of distinct new departures in pigeons and poultry we have given examples, but Professor J. E. Duerden, an acknowledged expert on ostriches, writes (1919) as follows : " Without any hesitancy it can be affirmed that in the course of the fifty years during which the ostrich has been domesticated, it has never produced a feather variation, germinal in its origin, such as could be regarded as of the nature of a sport or mutation. . . . The greatest mixture of germ-plasm is going on, but no single hereditary factor or determiner is altered in the process, and has not altered throughout the history of ostrich breeding ; only new combinations are formed of factors already available." Professor Duerden allows that some degenerative phenomena are observable, *e.g.* in the reduction of toe-scales, but he will not admit the occurrence of anything positively new, with, perhaps, one exception.

The one new departure which Professor Duerden has observed (1918) is the occurrence of 42 plumes in the first row of the wing. This was observed in two birds, one of which survived and bred true. From a quantitative variation of this sort it may be possible to raise a stock which would give the same number of feathers from fewer birds. The average number of plumes in the first row is 36.54 throughout Africa, the range being 33 to 39 ; the selection

that has gone on during fifty years of ostrich-farming has affected the quality of feathers but not the quantity. Indeed, Professor Duerden believes that the wing of the ostrich is degenerating as regards the number of feathers, the 42-plumed wing being interpreted as a hark-back to an ancestral condition, just as a guinea-pig sometimes shows four toes instead of the normal three. It is pointed out in this connection that the third finger of the ostrich is almost buried in flesh, and that it bears no claw as is often alleged.

Terminology.—When we carefully examine a large number of specimens of the same kind—sparrows let us say—we find that they are very far from being all alike. They differ from one another in details, just as we see among the members of a human family. These individual peculiarities can be measured and registered: they may be called “observed differences” or “observed divergences.” We need some term that will commit us to no theory.

A more intimate study of the observed differences shows that some of them are due to peculiarities in “nurture,” *e.g.* in habits, nutrition, and surroundings. These peculiarities directly due to peculiarities in exercise, diet, habitat and so forth are technically called “acquired characters” or, preferably, somatic modifications. They may be defined as structural changes in the body, acquired during the individual lifetime as the direct results of peculiarities or novelties in function, nutrition, and environment, and so transcending the limits of organic elasticity that they persist in the individual after the inducing conditions have ceased to operate. They are “exogenous” dints or imprints, hammered on from without, or they are direct parries of nurtural thrusts. The word “nurture” was used by Sir Francis Galton to include all manner of extrinsic influences that play on the body, in contrast to the intrinsic hereditary “nature” which expresses itself in development. When the colour of the canary’s plumage changes in response to peculiar food, when the lining of the gull’s stomach changes when it turns from fish to grain, when the muscles of the breast degenerate in captive birds, we speak of somatic modifications. They

are often very important for the individual, but it is uncertain whether they can be entailed as such on the race.

Now when we subtract from the total of observed differences all that we can interpret as modifications, and when we also put aside differences due to age and sex, the remainder consists of inborn variations. These are due to novel permutations and combinations in the germinal material that developed into the organisms we are studying. Some novel arrangement or disturbance in the intimate architecture of the egg-cell and the sperm-cell, expresses itself in development as a variation or new departure—endogenous not exogenous, an outcome not an imprint. There can be little doubt that these germinal variations furnish by far the greater part of the raw material of evolution.

New departures or variations in the wide sense may be conveniently ranked in two groups : (a) continuous, quantitative variations, such as a slightly longer pinion or a slightly stronger bill, and (b) discontinuous, more qualitative variations, such as the loss or addition of a wing-feather, the gain of a crest or a spur. The former may be spoken of as *inborn fluctuations*, a little more of this and a little less of that, but they must be kept apart from similar changes (*acquired modifications*) which are due to peculiarities of individual nurture. The discontinuous variations, which occur brusquely, without grading into one another or into the characters of the parents, may be called *mutations*. What is inborn or germinal in origin is always *heritable*, unless it be an "impossible" variation like sterility ; but it does not follow that it is always "transmitted" or entailed. As a matter of fact the forthcoming evidence of entailment is stronger for mutations than for fluctuations, but this inquiry is still very young. On general grounds—the continuity of the germ-plasm—a variation in the germ-cells is likely to be continued in the inheritance unless it be of a disintegrative character, such as some pathological disturbance.

So far then, the terminology runs :—

Observed divergences	{	Germinal variations	{	Innate mutations.
		Somatic Modifications		Innate fluctuations.

PLATE IX



[Photo by Norrie, Fraserburgh.]

THE GREAT AUK AND THE LITTLE AUK.

The extinct Great Auk (*Alca impennis*), last seen about 1844. It was about 32 inches long and unable to fly. The Little Auk (*Alle alle*), a northern bird of rapid flight, holds its own. It is 8 inches long.

§ 4. ILLUSTRATIONS OF VARIATIONS

Fluctuations or continuous small variations may be illustrated in regard to the following characters (Allen, 1871, and Wallace, 1889) : the total full-grown size, the proportions of various parts, the relative lengths of feathers, the strength of particular muscles, the shape of the bill, the colour of the plumage. Allen measured 20-60 specimens of a large number of common American birds and concluded : " The facts of the case show that a variation of from 13 to 20 per cent. in general size ; and an equal degree of variation in the relative size of different parts, may be ordinarily expected among specimens of the same species and sex, taken at the same locality, while in some cases the variation is even greater than this." So there is abundant raw material on which natural selection might operate. Reference has already been made to the extraordinary abundance of slight differences in the coloration of guillemot's eggs, which must correspond to slight variations in the constitution or metabolism of the mother-bird. Lotsy speaks (1916, p. 92) of the collection of 200 specimens of buzzard (*Buteo buteo*) in the Leiden Museum, " hardly two of which are alike." He interprets the diversity as due to the fact that " no selection has been at work, because this bird of prey is so strong that it has practically no enemies in the regions in which it occurs." A famous instance of diversity is that of the ruffs ; the individuality of the male birds is extraordinarily pronounced, but all the females or reeves seem to be like one another.

Mutations or brusque variations may be illustrated by the sudden appearance of a white blackbird, or of a fowl with extra toes. Bateson (1894, p. 55) gives a good example in the Moorhen which occasionally appears as a " hairy variety." The feathers are destitute of barbules and consequently have a hairy texture, greatly changing the general appearance of the bird. " A few feathers of this kind have been found in Hawks and Gulls, and in the case of a Parra (a bird which

bears considerable resemblance to a Moorhen), a great portion of the body feathers were in this condition. The feathers of the Apteryx and Cassowary are also partially destitute of barbules. Mr. Gurney was informed of a single case of a Grey Brahma hen which showed the same peculiarity, which appears otherwise to be without parallel. The case of the Silky Fowl is similar in the absence of most of the barbules, but in it the tip of the shaft is produced to a delicate point, and the barbs are fine and sometimes bifid or trifold at the apex. The colour of the skin and bones is purplish blue." The "hairy moorhen" and the "silky fowl" may serve as good examples of mutations.

Professor Bateson (1913, p. 42) gives another interesting case among the Honey-creepers or Sugar-birds (*Coereba* or *Certhiola*) of certain West Indian islands. They are small birds about the size of a nuthatch, with a general colouring of black, yellow, and white. Many of the islands have types peculiar to themselves, as is usual in such cases. From the island of St. Vincent the Smithsonian Institution received in the late seventies of last century several completely black specimens in addition to two specimens of the usual yellow and white "type." The black bird conformed to "the type" except that the yellow pigment was obscured by black; it was a "melanic" mutation. It is interesting to find that, as is happening with some melanic moths, the dark mutation is replacing "the type." The yellow type is now nearly or perhaps actually extinct; the black form is one of the commonest birds on the island. This case illustrates the meaning of a mutation, and it also shows how a mutation may succeed.

There are many hints of species and varieties arising by mutation, but the fact must not be overlooked that there are other series of species among birds which strongly suggest that evolution may sometimes have occurred by small steps and slow stages, that is to say, without mutation. Thus Dr. C. B. Davenport refers to the wide-ranging species of the North American song-sparrow (*Melospiza*) which form a graduated series, very different at the extremes.

§ 5. POSSIBLE ORIGINS OF VARIATIONS

It is not difficult to understand how certain kinds of variations may arise, namely in the course of the life-history of the germ-cells which includes several notable opportunities for permutations and combinations.

In the case of many heritable characters it seems certain that they are represented in the egg-cell or the sperm-cell by material items of some sort, usually called "factors" or "genes." These are the *initiatives* in the germ-cell which develop into the *characters* of the adult, after the usual trafficking with the appropriate "nurture." In some cases it is certain that these "factors" lie in a longitudinal series in the nuclear rods or chromosomes of the nucleus of the germ-cell. By observations, as patient as they are ingenious, it has been found possible in certain cases to map out the chromosome, and to say "the factor for eye colour lies about the centre of the third chromosome"!

Now in the history of the egg-cell there is a process of nuclear maturation, during which half of the chromosomes are expelled—forming what is called the first polar body, which comes to nothing. The number of chromosomes in the nucleus of the egg-cell is reduced to half the normal number, and the same reducing (or meiotic) division occurs in the history of the sperm-cells, so that the ripe sperm-cell has also half the normal number of chromosomes. In

fertilisation the normal number is restored: $\frac{n}{2} + \frac{n}{2} = n$.

Returning to the ripening egg-cell, we must notice that the chromosomes lie in what are called "homologous pairs," one of which is believed by many to be, to begin with, of paternal origin, and the other of maternal origin. In any case they contain similar sets of factors, and in their close approximation there is sometimes a strange "crossing over," a block of the one chromosome exchanging with a block from the other—which might of itself lead to some new permutation if the corresponding blocks are not quite identical.

Let us suppose that in a pair of homologous chromosomes, one (A) has a factor (x) for a particular kind of iris pigmentation, which the other (a) has not. When the first polar body is formed, it will take with it either A or a . If it takes A and therefore x , and if the ripe egg is fertilised by a spermatozoon also without x , the resulting offspring cannot have the particular kind of iris pigmentation for which x was the germinal representative. In another egg the polar body may remove the chromosome a .

If we compare the inheritance to a pack of cards, each card representing a chromosome, there is a throwing away of half the pack in the maturation of the egg. There is a corresponding reduction in the history of the sperm-cells, which are divided into two sets, each set with a different half-pack. In fertilisation the egg's half-pack and the sperm's half-pack form a complete pack once more.

The facts are intricate, but the general idea is clear that in the history of the germ-cells, there are various opportunities for shuffling the cards—for permutations and combinations among the genes. Among these opportunities we notice the chance of "crossing over," the reduction-divisions of maturation, and the re-combining in fertilisation.

But what can one say of qualitative variations which suggest something more than "shuffling"? What can one say as to the origin of the qualitatively new? Perhaps the less said the better, since the answers are almost wholly speculative. What might induce changes in the genes themselves or what might lead to the origin of a new gene?

The living germ-cell is a potential organism; it has within it the gains of the ages; it is a treasure-house: perhaps like other living things it has an intrinsic capacity for re-arranging and re-organising itself. Perhaps the trigger of its variability may be pulled by deeply saturating environmental changes, such as the setting in of an ice age. Perhaps the complexity of the germ-cell may be disturbed and re-arranged by changes in the nutritive streams of the blood and lymph. But the origin of the distinctively new remains the most difficult problem in biology.

To make more concrete what is meant by a germinal disturbance expressing itself in a bodily variation, we may take a particular case reported by Dr. Oscar Riddle (1917). From an egg produced under the weakening influence of "reproductive overwork" a female pigeon was hatched which showed for a while a marked lack of control over the voluntary movements of the head and body. This practically disappeared in the adult, but when the affected female was paired with two different males the derangement reappeared in the progeny and continued through four generations. It was a sort of hereditary ataxia, and behaved, with some irregularities, as a Mendelian recessive. Thus out of 175 young pigeons reared to the age at which the disorder might be exhibited, 119 were classed as normal and 46 as affected. A subsequent study by Mathilda L. Koch and Oscar Riddle (1918) indicated that the disordered brains were suffering from a chemical under-differentiation or immaturity. But the immediate point is that a germinal defect, originating in "reproductive overwork, expressed itself in a hereditary brain disorder." The disorder is exhibited in all degrees and has been inherited undiminished to the fifth generation.

As an instance of what is meant by linkage of variations we may refer to the close correlation which is seen in certain strains of poultry between brachydactyly (reduction of the size and number of joints in the toes) and the presence of feathers on the instep region. The two peculiarities (and probably coalescence of toes or syndactyly) seem to be linked together, and are perhaps dependent on one and the same factor, the nature of which is obscure (Danforth, 1919).

The problem of the origin of the new is far from solution, and the difficulty of the problem is emphasised by the range of new possibilities which the concept of variation includes. A variation may mean a feather less in the wing or twelve feathers more in the tail; it may mean a white blackbird or a black sugar-bird; it may mean a lengthening of the leg or a strengthening of the wing-muscles; it may be the beginning of webs on the toes or of a gizzard in the stomach. But a variation may be quite different from any of these—

it may be an increase in constitutional vigour, a lengthening of life, a change in the rhythm of metabolism, a change in the activity of a regulatory gland, an increase or decrease in reproductivity, a change of habit towards activity or sluggishness, an experiment in behaviour, the waning or waxing of an instinct. It may also mean the lengthening out of one chapter of the life-history, *e.g.* brooding, and the telescoping-down or even suppression of another, *e.g.* nest-making.

§ 6. MODIFICATIONS IN BIRDS

As we have explained, the word "modification" is used in a technical sense by many biologists to denote changes that are wrought on the individual as the direct result of peculiarities in nurture, *i.e.* in environment and food, in use and disuse. They are dints or imprints which persist after the inducing causes have ceased to operate, but there are very few cases where there is even a hint that they can be entailed on the offspring either as such or in any representative degree.

John Hunter and others have shown that the walls of the stomach of gulls and some other birds may be experimentally altered by a change of diet. If the food be made harder, the wall of the stomach assumes more of a gizzard character. If the food be made softer, there is a relative increase of the soft part of the stomach. The experiment is made annually in the case of the Herring Gull which has a harder stomach in summer when it is eating a considerable quantity of grain, and a softer stomach in winter when it is subsisting largely on fish. There is unwelcome evidence in the North of Scotland that the Herring Gull is taking more and more to vegetarian diet in the farmer's fields. If we suppose this new habit, fortunately punctuated by the seasons, to become more and more habitual, it is plain that in the course of time, those gulls would succeed best which had greatest plasticity in the temporary adjustment of their stomach-walls to diversified diet. There is no doubt as to the individual

modifiability; but we do not know of any convincing evidence to show that this reperccuses on the race.

The colours of birds' feathers may be altered notably by a change in their food, as in the case of canaries and parrots. Mr. C. W. Beebe has shown that some birds, such as the Bobolink, may be dieted so that they keep their breeding plumage throughout the year and may sing their spring song in mid-winter. This is a remarkable modification.

Modifications are common among birds on a small scale at least, and they may affect rather subtle qualities such as fecundity (the egg-laying of poultry), fattening, and power of flight. But while they may be of much individual importance, it has not been proved that they directly affect the race. In other words, we do not know that they are transmissible. The ancestral jungle-fowl will lay at the most 40-50 eggs in its lifetime, while a domestic hen of superlative egg-laying quality may lay 3000! This is partly due to stimulating nutrition producing its effect afresh on successive generations of *individuals*, and partly to the selection of strains of high fertility.

It is easy enough to *interpret* a peculiarity in a bird as due to the cumulative transmission of bodily modifications (or individually acquired characters), but it does not follow that the peculiarity in question arose in that way. The burrowing parrot, Stringops, has ceased to fly, and the keel on its breastbone is practically absent. It is easy to interpret this as due to degeneration following disuse of the muscles of flight, but what actually happened may have been very different. It may be that the ancestors of the present-day Stringops suffered from a constitutional variation in the direction of weakened muscles and dwindling keel, and that they therefore took to burrowing. This is one of the continually recurrent dilemmas of ætiology, and the only solution is along the lines of open-mindedness and active scepticism.

It has often been said that the hereditary occurrence of callosities on appropriate places of an animal's body points

to the transmission of individually acquired modifications. To this it may be answered that callosities sometimes appear as a species-character in places where they are not known to be of any use, and that these callosities must be regarded, like many other integumentary peculiarities, as bodily expressions of a germinal variation. If this be granted, it may be allowed that callosities in appropriate places may have arisen from germinal variations which happened to be useful or adaptive. In other words, they may represent outcrops from within rather than indents from without. It is also possible that a callosity may be the necessary growth-correlate of some much bigger variation in conditions of skin-pressure, blood-vessel distribution, and innervation.

A concrete case of interest is to be found in the two-toed ostrich (Duerden, 1919). When the ostrich is crouching, it rests on the tips of its partly bent toes and on the upper (ankle) end of its instep (tarso-metatarsus). Now there are callosities on the toes and on the ankle, which are doubtless parts of the inheritance, for they occur on chicks before hatching. It might be concluded that these callosities had become part of the inheritance through the transmission of the results of pressure on the skin during the individual lifetime. But things are not so easy.

It appears that the median ankle callosity is not used—nowadays at least—though it continues to be part of the inheritance. If it be urged that it may have been of use once, a further difficulty comes into view. Besides the median ankle callosity, there is an accessory ankle callosity, which begins to form after hatching and gradually becomes larger and coarser. This accessory pad seems to be of much use, but it is not known to be transmissible. Professor Duerden ingeniously suggests that the ostrich has ceased to be plastic. “In many respects the ostrich appears to have reached senility [in a racial sense], and it may be that structural changes resulting from external stimuli are now more likely to remain transient, instead of becoming impressed permanently upon the organism. This may assist in some measure in understanding why the later

accessory ankle callosity has not become hereditary, and also why the median callosity, though unused, continues to appear generation after generation." It is no reproach to say that this is purely speculative biology—only it remains unconvincing.

A number of experiments have been made on different kinds of animals as to the effect on the progeny when the parents are liberally treated with alcohol. The results are rather discrepant; the alcoholisation seems to be very deleterious in some cases, *e.g.* guinea-pigs, but not so in other cases, *e.g.* fowls. The experiments made by Raymond Pearl (1917) showed relatively little bad effect in poultry. He used pure-bred Black Hamburg cocks and pure-bred Plymouth Rock hens, which were subjected to vapour of ethyl-alcohol, methyl-alcohol, or ether in inhalation tanks, the treatment extending over an hour each day, for 130–354 days, with a mean of about seven months. The full brothers and sisters of the "treated" birds were used as controls.

The results show that "the treated animals are not conspicuously worse or better than their untreated control sisters or brothers. The survivors, *i.e.* those not killed by accident, after roughly a year and a half of daily treatment, are becoming a bit too fat for their best physiological economy, but except for that point, and the reduced activity which goes with it, they are very much like normal fowls." At the end of the experiments the treated hens were on the average 9.9 per cent. heavier than their untreated sisters.

In a subsequent paper, Pearl states that after alcoholic treatment of the parent fowls: the pre-natal mortality of the embryos was reduced; the post-natal mortality of the chicks was reduced; the sex-ratio was not sensibly affected; there was no significant difference in mean hatching weight when only the male parent was treated; the offspring of alcoholised parents showed a mean hatching weight and a mean adult weight higher than that of normal birds; the proportion of abnormal chicks was not greater than usual; many germ-cells of the alcoholised parents did not form zygotes (fertilised ova), but those that did were not defective

in any way. The only deleterious symptom was that the proportion of fertile eggs in the matings of alcoholised parents was below the normal. This last fact suggests that alcohol and similar substances act as eliminative agents upon the germ-cells of the treated animals, probably discriminating between different types of ova or spermatozoa.

The mortality among the treated hens was much smaller than among the untreated control sisters. Neither the total amount of egg production nor its distribution was significantly different in the two sets of birds. Both the treated birds and the controls laid normally and well.

It must be noted that the number of birds used was small, but subsequent experiments were made. It may also be that the "treating" was too moderate to be of bodily importance to the individual.

According to O. Riddle and G. C. Basset (1916) a prolonged treatment of hens with alcohol by the inhalation method reduces the size of the yolk, and the effect persists for weeks or months.

Numerous experiments have been made by A. Magnan (1914) on the mechanical and chemical effects of different diets on young ducks of the same brood. The naturally omnivorous birds were able to thrive on insects or fish, on flesh or vegetables. It was found that a vegetable diet considerably increased the surface of the digestive canal, while a flesh diet reduced it. The cæca and the short large intestine were most developed in the vegetarians. The weight of the intestine increased in those fed on hard food and fish, for the muscular wall increased in thickness. This was particularly noticeable in the case of fish-fed ducks, though the intestinal wall was not the largest. The weight and surface of the proventriculus increased in proportion to the size of the prey. This is a purely mechanical effect and was well-marked in the fish-eaters.

Some chemical effects of the modified diet were also observed, notably in the liver. Fish-diet and insect-diet caused hypertrophy, but a pure flesh-diet and a pure vegetable-diet both caused a reduction in the weight of the

liver. The same was true in regard to the kidneys, pointing to a greater toxicity of fish and insect as compared with flesh and vegetable food.

A flesh-diet proved the best as regards growth, and the best even in adult life, though less markedly so. Insects were nearly as nutritive as beef during growth, but in adult life they proved inferior. Fish and vegetables were less well suited for the younger stages, but in adult life vegetables proved only slightly inferior to beef. Laying began earliest and was most abundant in the fish-fed birds.

Magnan points out that the modifications brought about in the ducks by each kind of diet correspond in general to the features seen in birds whose natural diet is like that in the experiment. This would indicate that diet may have a considerable influence on the character of the food-canal in the individual bird, but behind this there is probably the fact that in the course of selection that kind of food-canal has been established which is best adapted to the customary diet.

A very important contribution to the question of the transmissibility or non-transmissibility of individually acquired somatic modifications has been made by Professor M. F. Guyer and E. A. Smith (1918). It is quaintly subtle, but it is more value than much discussion. Its introduction here is justified by its importance and also because the *corpus vile* was the fowl. Lens tissue from rabbits and mice was made into an extract and injected into fowls. It excited in the blood of the fowl the production of specific anti-bodies, that is to say, chemical counteractives to the deleterious intrusions. Now, if the serum of the fowl's blood be injected into pregnant rabbits, the anti-bodies may attack the lenses of the unborn young, producing a liquefaction, apparently dissolving a fibrous protein in the lens. The reaction is not invariable, however, since the majority or even all of the individuals of a litter may escape the cell-dissolving (cytolytic) anti-bodies; and even when an individual embryo is attacked one eye may escape. This is difficult to explain. No effect was observed in the mother

rabbit, which may be due to the meagre circulation of the blood in an adult lens. But the issue is important: a specific modification of the lens was induced in the young *in utero* by means of a peculiarly sensitised serum, and the deleterious effect on the lens was observed in a second generation of rabbits developing without interference.

§ 7. MODIFICATIONAL SPECIFIC CHARACTERS

It is highly probable that some of the differences between species or varieties are purely modificational or nurtural, that is to say, that they are impressed on each individual by some peculiarity in environment, nutrition, or function. The well-known newt, *Proteus anguineus*, of the caves of Carinthia, Carniola, and Dalmatia is destitute of pigment, and no specimens in the caves have ever been found that were otherwise. It might be thought that the wan white colour was a definite specific character, an ingrained constitutional defect. But it is well known that if specimens are brought out of the darkness and kept in the light they rapidly put on pigment. The absence of pigment in the cave specimens is not due to any constitutional defect, it is due to the absence of light which is necessary as a liberating stimulus for pigment formation.

Linnets from California were introduced about half a century ago into the Hawaiian Islands. In the United States the usual colour of the males after the post-juvinal moult is red, in those parts of the plumage which are brightly coloured. There occur rather infrequently, irrespective of locality, individuals of three other colours—yellow (most rarely), orange, and red with yellow or orange feathers intermixed. Now Mr. Joseph Grinnell points out (1911) that male linnets in Hawaii are all of the yellow or orange type of coloration, and that is in some way due to the island habitat. It is not possible to say what the stimulus is, though Grinnell thinks that it is not a very obvious one, or what is lacking in stimulus; but it need not be anything very momentous. For it seems that the difference in colour

simply means physiologically that the amount of ferment produced in the feather-germ is insufficient to carry on the oxidation of tyrosin beyond the yellow, or at farthest, the orange state. It may be that inbreeding has accentuated a slight constitutional defect, but it seems more likely that the off-colour character is purely modificational, *i.e.* impressed on each individual, generation after generation.

§ 8. DIRECTIVE FACTORS : PROCESSES OF SELECTION

Professor Davenport tells us the story of chickens which he had in a field near the Cold Spring Harbour Institute for Experimental Evolution. Of the 300 there were 240 white or black and conspicuous, and 60 spotted and inconspicuous. In a short time 24 were killed by crows, but only one of these was spotted. This is a simple and clear instance of the operation of discriminate selection. There was survival value in being spotted. In the course of time, had the field been Nature, the race of fowls would have contained only spotted and inconspicuous forms. The evolution of the species would be directed by selection.

Professor Bumpus (1898) relates an interesting observation on the house-sparrow in the United States. After a severe storm 136 were picked up and brought into the laboratory, where 72 revived and 64 died. The survivors and the eliminated were then carefully measured as to length, size of wing, weight, length of head, length of humerus, femur, and tibio-tarsus, width of head, and length of breastbone. For all but the last of these characters the range of variation was considerably greater in those that succumbed. The extreme variants, *e.g.* those with longest as well as shortest wing-span, were eliminated. The survivors were a little shorter, lighter, longer in the leg, the humerus, and the breastbone. But the essential characteristic of the survivors was *general stability of structure*. Now severe storms are of frequent occurrence, and if they do not overpass a certain limit (when all the birds will perish and the elimination will

be indiscriminate), the tendency will always be towards the survival of those of more stable constitution.

There are many modes and levels of Natural Selection, and Darwin always laid emphasis on its manifold and subtle operation. It is useful to distinguish *lethal* selection, which works by eliminating the relatively less fit to given conditions of life, from *reproductive* selection which works through the predominant increase of those that are at once relatively fit and relatively fecund.

In his shrewd realisation of the subtlety of many selective processes, Darwin saw, for instance, what some of his successors have missed, that the sifting need not involve a sudden cutting off of the relatively less fit, since a shortened life and a less successful family will in the long run bring about the same result as a drastic pruning.

Darwin also realised, what some of his successors have missed, that even slight peculiarities may be of critical moment when tested in relation to the complex web of life in which the creature has its being. This is of great importance in regard to the general progressiveness of evolution—that new departures or variations are sifted in reference to a slowly elaborated and firmly established system of inter-relations. There has been an evolution of sieves as well as of the sifted. And that way progress lies.

As a modern instance of *artificial* selection we may take Raymond Pearl's experiments (1915) towards improving the winter production of eggs in fowls. The capacity for laying well in winter seems to behave like a Mendelian character, depending upon two factors or genes, one of which is sex-linked.

For a time the method pursued was that of selecting out hens with a high egg record, but this did not yield very promising results. What proved effective, however, was selection based on the egg-laying performance of the progeny. The reason for this is plain, that a bird might be itself a high layer without having the quality of high fecundity as an integral part of its hereditary make-up. A sure diagnosis of the hereditary constitution can only be made by means of the

progeny test, and rapid progress was secured when those individual birds were sorted out whose offspring proved themselves high-producers. To put it in another way, individual high-laying may be in part modificational; when it re-appears in the progeny it must be regarded (unless modifications are transmissible) as variational. What the selection did was not to change the constitutional fecundity, but to change the constitution of the poultry population by rejecting those whose progeny were not high-layers.

Germinal Selection.—There is some interesting evidence in support of the view that there may be a process of selection among germ-cells, so that if they are not alike those with certain congeries of hereditary factors survive while others with a different make-up succumb. One of the lines of evidence is curious (C. H. Danforth, 1919). Heterozygous fowls, that is to say with different kinds of germ-cells, were subjected to alcohol vapour. The relative proportions of certain traits, such as brachydactyly, polydactyly, and white colour, were different from the proportions produced by similar hens in normal conditions. This looks as if the alcohol vapour eliminated certain types of eggs in the ovary. If, then, the survival of germ-cells is determined in abnormal conditions by the genetic or factorial make-up, the suggestion rises whether in normal conditions also the combination of hereditary factors may not have a survival value, which allows some types to be launched on the voyage of development while others are destroyed on the slip. This suggestion of Danforth's appeals to us strongly, for there are various reasons for thinking that the harmony and viability of the future explicit organism is conditioned at the start by the harmony and viability of the implicit organism—the germ-cell.

If a toxic agent, such as alcohol, selects between the different kinds of germ-cells, and if this selection be sustained consistently for generations it would tend to result in orthogenesis, *i.e.* variation in one direction. Dr. Danforth mated cocks heterozygous in regard to brachydactyly, polydactyly, colour, and shape of comb with hens homozygous for these features in their recessive forms. A record was made of

the numbers of each class of young produced. Then the cocks were subjected to alcohol inhalation, and thereafter mated again. The record of the different number of each class of young produced was different from before, indicating that the administration of the alcohol altered the proportions, and this could be done only by a discriminate selection of certain classes of spermatozoa.

§ 9. ISOLATION AND THE REVERSE : IN-BREEDING AND OUT-BREEDING

There is another directive factor in evolution, which operates on variations that crop up. This factor is called "isolation," and it includes all the means that restrict the range of inter-crossing within a species. The barriers may be spatial, as when a peninsula becomes an island, or temporal, when different members of the species become mature at different times. They may be habitual, when different members of the species adopt different ways of living. They may be physiological, when differences in size, for instance, prevent crossing between dwarfs and giants. They may be psychical, *e.g.* when different varieties, say of pigeon, show marked preferences in their mating, seeking out sometimes those of their own colour. As examples of isolation among birds we may cite the case of the Golden Warblers of the West Indies, for each well-separated island seems to have its own form or species. Similarly, each island in Hawaii has its own species of a number of genera of Drepanine birds.

Isolation as a factor in evolution must operate in two ways, for we cannot separate a shortening of the radius of possible crossing from a lengthening of it. When a peninsula becomes an island by a coastal depression there is a reduction of the possible inter-crossings among the members of a species. When a coastal elevation joins an island to the mainland there is an increase of the possible inter-crossings.

On the one hand, there is increased in-breeding or endogamy, which tends to make a stock more homogeneous

and more stable. On the other hand, there is increased out-breeding or exogamy, which tends to promote variations and divergence. There can be no doubt that alternations of in-breeding and out-breeding have played an important part in the evolution of birds, as in the case of other animal races, and in human history as well.

§ 10. BIRDS AND HEREDITY

Germinal Continuity.—The largest fact in regard to heredity (the genetic relation between successive generations) is that like tends to beget like. This is due to “germinal continuity.” Let us suppose a fertilised egg-cell with the implicit qualities *abcxyz*; it divides and redivides to build up a body in whose cells there is division of labour, some showing more of the quality *a*, others more of the quality of *z*, and so on. But while this body-making is going on, certain cells do not share in it, but remain undifferentiated, preserving intact and uniformly the potential qualities, *abcxyz*. These are the reproductive cells—let us say the eggs. And if one of these is liberated, with the original qualities unchanged, it will naturally develop into a creature like the parent. In each development, as Weismann said, a portion of the specific germ-plasm contained in the parent egg-cell is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation. This is the fact of germinal continuity and the reason why like tends to beget like.

In the early days of embryonic development in birds there is a segregation of the germ-cells that form the beginning of the reproductive organs. The distinction between body-forming cells and germ-cells is well defined. In other words, the germinal continuity is clear. We no longer ask whether the hen makes the egg or the egg the hen. The true statement is that the fertilised egg develops into the bird *and* the germ-cells thereof—egg-cells or sperm-cells as the case may be,

Unit-characters and their Factors in the Inheritance.—

One of the great modern discoveries is the proof that an inheritance consists, in part at least, of well-defined, relatively stable, hereditary items. These have received various names—factors, genes, or determinants. They are differentiations in the germ-plasm corresponding to well-defined, clear-cut characters in the offspring which are called “unit characters.” These are features which do not usually blend or intergrade, which are either there intactly or not at all, which are independently heritable. A particular colour of iris, a particular pigment in the plumage, a crest on the head, a spur on the foot, an extra toe, a great length of tail feather, may be a unit character, which has its correspondent in the germ-cell in a particular “factor” or “gene.” It may be, however, that several factors combine in the production of a character (*e.g.* coloration), or that one factor has to do with the development of several characters, just as the same disease-taint may find expression in several different organs.

A “character” in a full-grown organism is some well-defined, measurable feature, such as the colour of the iris, the nature of the comb, the presence of a crest on the head, the number of quills, the nature of the stomach, the size of the keel on the breastbone, the number of toes, and so on. In the strict sense the inheritance consists of the “factors” or “genes” corresponding to these characters, and not of the characters themselves. It is necessary to insist on this (though it may be pedantic to reiterate the distinction), for one factor may affect several characters, and one character may imply the co-operation of several factors. But, more than this, the fully formed character is always the product of the inherited “nature” and the appropriate “nurture.” The expression of a “factor” in development depends in some measure on the fullness of the “nurture”—meaning by this technical term of Galton’s all manner of influences in environment, nutrition, use and disuse. Peculiarities in “nurture” often involve peculiarities in the development of a character; on the other hand, some peculiarity in a character may be due to some novelty in the “factors.”

The most important point in regard to the factors of unit-characters is that they behave in heredity as if they were definite entities, like the radicals in chemistry, which can be shuffled about and distributed to the offspring in some degree independently of one another.

Different Modes of Inheritance.—There are various possible results when two birds are crossed.

(a) The offspring of two pure-bred birds which are very like one another may be practically indistinguishable from the parents. This is complete hereditary resemblance.

(b) The offspring of two divergent birds (within the same species, of course) may be something distinctly novel. It may show a mutation. This is the other extreme.

Between these two extremes there are three possibilities.

(c) The offspring may be a blend as regards certain characters between the two parents; and among domesticated birds the occurrence of what looks like blending is not uncommon. Whether what looks like blending inheritance is really such cannot be determined without data in regard to the next generation. One requires to know whether all the grand-offspring show the appearance of blending that the offspring exhibited.

Dr. Ernest Warren (1914) has described two hybrids between two kinds of cockatoos, belonging to different genera—*Cacatua galerita* (male) and *Licmetis nasica* (female). The hybrids seemed to show some blending of the characters of the two parents. Out of ten characters the hybrids were nearer *Cacatua* in five, nearer *Licmetis* in one, and almost exactly intermediate in four. In every character examined, with the possible exception of the coloured and non-coloured lores (the space between the bill and the eye), there was a very obvious blending of the paternal and maternal characteristics. But we require to know more about such cases. When a character owes its development to the co-operation of several "factors," the offspring might have some of these from the mother's side and the rest from the father's side, so that the character appeared as a blend although no maternal factor was affected by a corresponding paternal

factor, which is what true blending implies. It is necessary to have further data in regard to the next generation.

The results of crossing different species of birds seem often to point to what may be described as "blending." Thus John C. Philipps reports (1915) crosses between pintail and mallard, *Anas tristis* and mallard, and Black East India duck and mallard, in which one of the outstanding results was that many characters, apparently clear-cut and antagonistic, do not segregate clearly. On almost every feather region the minutest details of pattern and colour show the influence of both parental races. It is otherwise in hybrids between distantly related forms. Some of the particular results of species-hybridisation are interesting. Thus if only one of the species is sex-dimorphic, a more primitive type of male plumage occurs in the hybrids. Hybrids between mallard and black duck showed a condition closely resembling eclipse or summer plumage.

(d) It very occasionally happens that the offspring exhibits a feature not seen in either of its parents, but characteristic of a distant ancestor. This is described as reversionary inheritance or harking back, and it may be illustrated by the case of a Rock-dove type suddenly appearing as the result of an unfortunate cross between two discrepant breeds of pigeon. Thus Professor Cossar Ewart (1899) reports an experiment in which a pure white fantail cock pigeon, of old-established breed, which in colour had proved itself prepotent over a blue pouter, was mated with a cross previously made between an "owl" and an "archangel," which was far more of an "owl" than an "archangel." The result was a couple of birds, one of which resembled the Shetland rock-pigeon and the other the blue rock of India. Not only in colour (slaty-blue), but in shape, attitude, and movements, there was an almost complete reversion to the form which is believed to be ancestral to all the domestic breeds of pigeon. The fact was there, and what was seen may be *described* as a reversion. It does not follow, however, that what occurred was a re-awakening or re-habilitation of long dormant hereditary traits characteristic

of the ancestral rock-dove. As will be made clear in connection with Mendelian inheritance, there is a more probable explanation of what happened.

Professor Ewart also reported that a dark bantam hen, crossed with an Indian game Dorking cock, produced amongst others a cockerel almost identical with the Indian jungle fowl (*Gallus bankiva*), which is the ancestral wild stock of domesticated fowls. This recalls Darwin's case of crossing a white Silky hen with a black Spanish cock, for there was among the progeny a cock that looked like a rehabilitation of the original wild *Gallus bankiva* type.

When the offspring resembles not its immediate parents, but one of its grandparents, the term reversion is quite inappropriate; such a frequent occurrence as "skipping a generation" admits of a ready Mendelian interpretation, as we shall presently see. Let us now turn to the fifth possibility, (e) *Mendelian Inheritance*.

Mendelian Inheritance.—There are three fundamental ideas in Mendelism. The *first* is the idea of "unit characters" already referred to—non-blending, crisply defined characters which are continued in at least some of the descendants as definite wholes, neither merging nor dividing. Now, as Professor Punnett puts it, "unit-characters are represented by definite factors in the gamete [or germ-cell], which, in the process of heredity, behave as indivisible entities, and are distributed according to a definite scheme. The factor for this or that unit-character is either present in the gamete or it is not present. It must be there in its entirety or be completely absent."

The *second* fundamental idea in Mendelism is that of dominance. When a crested fowl is crossed with one without a crest, the offspring have crests; the crest is called the dominant character and the absence of a crest is called recessive. But what makes one character dominant and another recessive we do not know. The character of having extra toes in poultry is dominant, and that of having normal toes is recessive. Broodiness is dominant, its absence recessive. Rose comb and Pea comb in fowls are dominant, while a normal comb is recessive.

To return : if a crested fowl is crossed with one without a crest, the progeny are all crested. This is expressed in the formula

$$D \times R$$

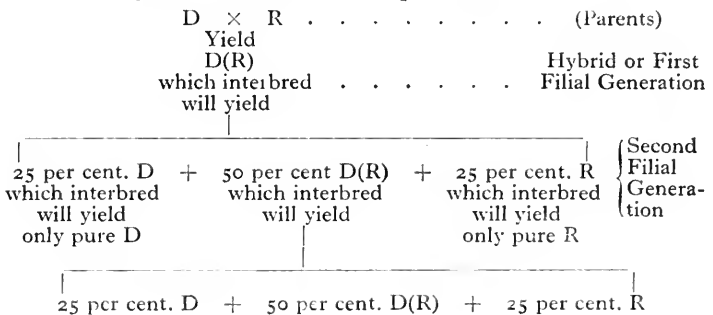
yields
D(R)

The recessive character is indicated in brackets beside the dominant character, because the next generation shows that it is not absent from the inheritance. It is represented by a factor in the fertilised egg-cell, though it may not find any expression in the body. Should it find a slight expression in the body, as it often does, then we speak of imperfect or incomplete dominance.

Now if the hybrid offspring D(R) be paired together or with others of precisely similar history, their offspring (the second filial generation) will be 25 per cent. pure dominant, 50 per cent. like the hybrids, and 25 per cent. pure recessive. In the case mentioned, there will be 25 per cent. pure-crested, 50 per cent. crested, but not pure-crested, and 25 per cent. pure non-crested. In external appearance there may be no difference between the pure-crested and the impure-crested, but there is a difference in their germ-cells, for the pure-crested, when paired with others of similar history, will yield only pure-crested, whereas the impure-crested, when paired with others like themselves, will yield the same characteristic Mendelian proportion

25 per cent. pure-crested + 50 per cent. impure-crested + 25 per cent. pure-uncrested.

To complete the schematic expression :—



In many cases, as we have noted, the dominance in the hybrid offspring (F_1) is not complete. Thus, if a black

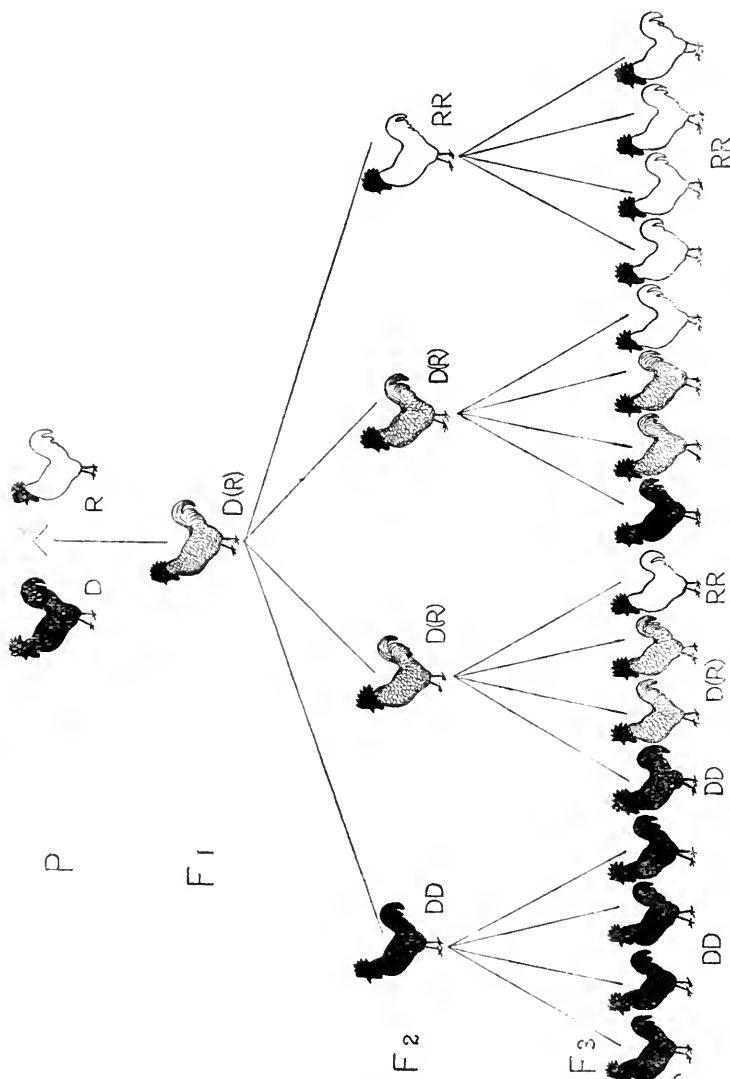


FIG. 58.—Inheritance in Andalusian Fowls. Letters as in text.

Andalusian fowl be crossed with a white one the progeny are "blue" Andalusians—a sort of diluted black, D(R). If

these "blue" Andalusians pair together they yield in the next (F_2) generation, 25 per cent. blacks, DD, 50 per cent. "blues," D(R), and 25 per cent. whites, RR, with splashes of grey. It had long been known that "blue" Andalusians did not breed true, that they would not yield more than six "blues" to the dozen. But the reason for this was not clear until Mendelian inheritance was re-discovered about 1900. The "blue" Andalusians do not represent a true-breeding race, they correspond to D(R)'s. To get twelve blue Andalusians to the dozen it is only necessary to cross D and R, the black and the white.

It should be noted, perhaps, that the matter is rather more complicated than we have indicated, for besides the blue-splashed Andalusians there are blue self-coloured Andalusians (W. A. Lippincott, 1918). The condition in the blues is due to the combined action of two factors, one securing black pigment for every feather in the body, and the other acting on the distribution of the black pigment in such a way that a characteristic blue-grey appearance results.

The *third* fundamental idea in Mendelism is that of the segregation of factors in the germ-cells. When a fowl with a dominant character is crossed with a fowl with a recessive character, there must be in the fertilised egg-cell the factors for both the dominant and the recessive characters. Let us call these factors *d* and *r*. Only one of them, in typical cases, becomes expressed in the body of the offspring.

But the fertilised egg-cell gives rise to a lineage of germ-cells which should by hypothesis all show the factors *d* and *r*. What Mendel suggested, however, was that in the history of these germ-cells there is a segregation into two sets, half of them with the factor *d* and half of them with the factor *r*. In other words, each germ-cell is "pure" with respect to the factor of any particular unit-character. To put it concretely, if there are 100 ova produced, 50 will carry the *d* factor and 50 the *r*; and the same for the sperms. If the subsequent fertilisations are fortuitous, the Mendelian ratio 1 : 2 : 1 *must* result in the offspring.

Some Illustrations.—(1) Professor Punnett (1919) gives

the following clear case. If a member of a true-breeding race of Black Rose Comb Bantams be paired with another, the offspring will be like the parents. The germ-cells will be all alike in having a double dose of the factor for blackness. Similarly if two members of a true-breeding race of White

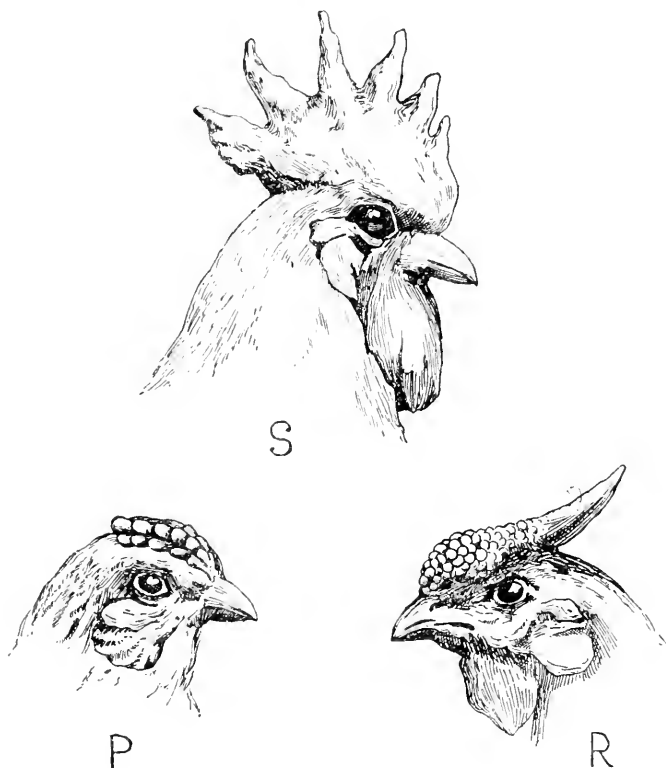


FIG. 59.—Combs of fowls. s., simple serrated comb; p., pea comb; r., rose comb.

Rose Combs are paired, the offspring will be all alike in having no pigment. It is usual to call such pure-bred offspring *homozygous*, which means that their germ-cells are all alike as regards the character in question.

But what will happen when White and Black Rose Combs are mated? The fertilised egg-cells will have the factors

for blackness from one side of the house, but not from the other. The offspring will all be black, for blackness is dominant in relation to whiteness. Now the germ-cells of these offspring will divide into two sets—one set carrying the factor for blackness and the other set not. It is usual to call such an organism *heterozygous*, which means producing two kinds of germ-cells. This duality of the germ-cells is sometimes demonstrable microscopically when half of the germ-cells carry a nuclear rod or chromosome with a distinctive appearance; but the idea of segregation into two contingents was arrived at as an inference from what happens when the hybrid offspring are paired. They yield, to the dozen let us say, 3 pure blacks (breeding true when mated with others like themselves), 3 pure whites (breeding true when mated with others like themselves), and 6 blacks, which are, however, heterozygous, and will when mated together yield the same ratios

$$3BB + 6B(W) + 3WW$$

(2) Fantail pigeons, as every one knows, have more than double the usual dozen of tail feathers. They are also without a preen-gland. Professor T. H. Morgan (1918) crossed fantails showing 29, 30, and 32 tail feathers with ordinary homers with 12, and the next generation (F_1) gave a range of variation between 12 and 20, the highest frequency being 14 feathers. "Evidently one or more of the factors of the fantail act as partial dominants, producing tails that have for the most part more tail feathers than has the common pigeon, but less than the fantail." In the next (F_2) generation there were many birds with a 12-feather tail, a good many had 14-16, a few approached the lower range of variation in the fantail (24-26). Professor Morgan also points out that it is probable that the hereditary factor (or gene) for more than 12 feathers, and that for no preen-gland, and that for white colour are linked together, which means that they are carried by the same chromosome.

(3) As an example of the subtle characters that are hereditary in definite ways, we may mention the refractive

index of the blood. It has been shown by Raymond Pearl and John W. Gowen (1914) that there is a definite, characteristic, and permanent difference between the refractive index of the serum of the common fowl (*Gallus*) and that of the guinea-fowl (*Numida meleagris*). When a genus-hybrid is successfully obtained (between common cock and guinea hen) it approximates in its refractive index to the guinea parent. In other words, as regards the physico-chemical constitution of the blood, in so far as that is expressed in the refractive index, the guinea-parent is dominant.

CHAPTER XV

BIRDS AND THE WEB OF LIFE

§ 1. Nutritive Inter-relations. § 2. Waves of Life. § 3. Reproductive Inter-relations. § 4. Parasites of Birds. § 5. Strange Linkages. § 6. The Hand of Man on Birds. § 7. The Inter-linking of Lives. § 8. The Conservation of Birds.

ONE of the great contributions Darwin made to science—and to man's way of thinking in general—was the concept of the web of life. Animate Nature is a vast system of linkages ; the circle of one life intersects that of another ; nothing lives or dies to itself. There has been evolved a complex system of inter-relations. As the philosopher Locke says, nothing is by itself, everything is a retainer to some other part of nature. How is this central biological idea illustrated in regard to birds ?

§ 1. NUTRITIVE INTER-RELATIONS

Carnivorous birds, like hawks and owls, play an important part in the economy of Nature by keeping a check on the increase of small mammals, such as rats, mice, and voles. Some of the plagues which spell ruin to man's farming and foresting are in part the nemesis of short-sighted or selfish destruction of birds of prey.

It must be admitted, of course, that birds do not confine their attention to mammals which are harmful from man's point of view, such as the rodents. An owl will devour a mole, and there would not be much need of mole-catchers if man had not interfered with the gradually established—though ever-oscillating—balance by shooting down birds of prey. It is plain, however, that rats and mice and voles are much more likely to be caught than weasels and shrews and moles. Therefore, birds of prey operate in the direction of progressive evolution. For we cannot

admit that it is merely anthropomorphism to regard the numerical ascendancy of poor-brained and almost spawning rodents as a faunal retrogression. A thousand mice will not compensate for the death of one mole.

No doubt some birds devour other birds; and when these "other birds" are insectivorous, so much the worse for man. It is difficult to over-emphasise the persistent insect-peril, for a few years of super-abundance among such insects as plant-bugs (Rhynchota or Hemiptera) would ruin the vegetation of the earth. And that would mean the degradation of the fauna and the rapid decline of man. We do not know whether the possibility is more than a theoretical one, for the foundations of Animate Nature have been well laid. But it is surely practical wisdom to lean one's weight against *interferences* which bring the insect peril nearer. The issues are so complicated that we doubt the wisdom of every big interference with birds, whether in the way of fostering or in the way of elimination, but if we had to choose between protecting a carrion-crow or a black-headed gull, we should vote for the latter. For the carrion-crow destroys many an insectivorous bird—we are not inclined to black-list or exterminate him on that account—whereas the black-headed gull eats huge numbers of "leather-jackets" and other injurious insect larvæ in the fields around the gullery.

When we come to birds that devour snakes, it is difficult to shunt off human prejudice. The fact is that the issue is mixed. We cannot get a clear bill. From the point of view of man and his stock (a narrow anthropocentric one) we praise the Secretary Bird—one of the masterpieces of creation—because it often kills snakes, which are hostile to human interests. But we must face the corollary that the elimination of certain kinds of snakes means the increase of rats and mice and other pests. Who is sufficient for these things? We cannot accept an entirely *laissez-faire* policy, first because no vigorous organisms that have achieved any success have ever done so, and second because man is rapidly making all Nature artificial, and he must

make good for such disastrous interferences as introducing rabbits into Australia or sparrows into the United States. What we plead for is careful scientific consideration of every step of interference ; what we protest against is everything in the way of drastic, artificial, wholesale elimination, as implied, for instance, in " big bags," for that is justified neither by science nor sport !

" There is an Australian story which reads as if written for man's instruction. On certain Murray River swamps several species of cormorants used to swarm in thousands, but ruthless massacres, based on the supposition that the cormorants were spoiling the fishing, reduced them to hundreds. But the fishing did not improve ; it grew worse. It was then discovered that the cormorants feed largely on crabs, eels, and some other creatures which devour the spawn and fry of the desirable fishes. Thus the ignorant massacre of the cormorants made for the impoverishment, not for the improvement, of the fishing. The obvious moral is that man should get at the facts of the web of life before, not after, he has recourse to drastic measures of interference " (Thomson, 1919, p. 88).

As regards the toll that birds levy on the lower Vertebrates (notably, Amphibians and Fishes), and on many Invertebrates (such as molluscs, spiders, insects, crustaceans and worms), we may safely say that the lower creatures can afford it. So far as one can understand the architecture of Nature, the abundance of minor creatures seems to form the foundation for higher expressions of life. The mosquito makes the swallow possible, and the midge the swift. This is not saying that mosquitos and midges were created in order that there might be swallows and swifts, yet the abundance of life among the lower forms of life has, as a matter of fact, made higher life possible.

Some of the tangles in the web of life are curious. Squirrels are often shot down because they destroy so many young trees, but an over-elimination of squirrels leads to an over-multiplication of wood-pigeons, on whose young squabs the ordinarily vegetarian squirrel levies useful

toll. And wood-pigeons do great damage on the farm by devouring corn and in other ways. The forester says, "Fewer squirrels"; the farmer says, "Fewer wood-pigeons." One is continually confronted with the difficulty of getting a "clear issue," for the circle of any animal's life cuts many other circles.

The mongoose imported to Jamaica to clear off the rats, did its work well, but thereafter it had to be fed, and it turned its attention to poultry and ground-birds, and to snakes and lizards, some of which devour insects. The thinning of the ranks of insectivorous ground-birds and reptiles meant an increase of injurious insects. And this is what actually happened.

Or again, it has been pointed out that bubonic plague often begins in Indian mills, where the workers eat their frugal meal in the courtyard. The inevitable "crumbs" attract rats, in whose blood the microbe of the plague is at home. A rat-flea, with fouled mouth-parts, leaves a rat and bites man, who is thus infected with the plague. If there was a dovecot whose inmates would promptly look after the "crumbs," there would be fewer rats, and less plague!

The success of sheep-farming may be linked to Pied Wagtails. For successful sheep-farming depends in part on the absence of liver-rot, a disease due to the parasitic liver-fluke. But the juvenile stages of this worm are passed within the little freshwater snail (*Limnæa truncatula*), which the Pied Wagtail is very fond of eating!

A few illustrations may be given of the way in which birds figure on both sides of man's account.

	+	-
Blackbird ..	Grubs	Fruit
Black-headed Gull ..	Many insects	Occasionally young fish
Bluetit ..	Many insects	Fruit-buds
Chaffinch ..	Aphides, insect larvæ	Fruit-buds and sprouting corn
Jackdaw ..	Leather-jackets, grubs, wire-worms	Young birds, eggs, peas, grain-crops
Rook ..	Leather-jackets, grubs, slugs, young voles	Fresh-sown seeds, young birds, eggs
Starling ..	Leather-jackets, wire-worms	Fruit
Thrush ..	Insects, snails	Fruit

Very careful observations have been made by Forbes on American birds, large numbers of specimens having been examined at different times of year. Two-thirds of the food of the American robin consists of insects, about 29 per cent. of garden fruits. Insects form 43 per cent. of the food of the catbird, fruits 52 per cent. Seventy-eight per cent. of the bluebird's food for the year consists of insects, 8 per cent. of spiders, 1 per cent. of millipedes, 13 per cent. of vegetable matter, including only 1 per cent. of fruit. Ninety per cent. of the food of the Kingbird consists of insects. Many birds are entirely insectivorous, and their usefulness in checking the multiplication of insects has been proved up to the hilt. This applies particularly to injurious insects, for they are apt to multiply in proportion to the abundance of food afforded by fields, plantations, and orchards (see Folsom, 1923, p. 239).

§ 2. WAVES OF LIFE

Wild Nature is in a state of moving equilibrium, like that of a top! There is no static balance, but an ever-oscillating adjustment. Usually, however, the oscillations in the old-established arrangements of eating and being eaten are within narrow limits, unless man interferes, or unless some big change occurs in climate and other physical conditions. When there is a succession of hard winters or of fine summers, the ripples may become waves. Let us take an instance from W. H. Hudson's "Naturalist in La Plata."

The summer of 1872-73 in La Plata was exceptionally fine—rich in sunshine and showers, blossoms and bees, and *mice*. In autumn the earth so teemed with mice that one could scarcely walk anywhere without treading on them; while out of every hollow weed-stalk lying on the ground dozens could be shaken. They were so abundant that the dogs subsisted almost exclusively on them; the fowls also, from incessantly pursuing and killing them, became quite rapacious in their manner; while the sulphur tyrant-

birds (Pitangus) and the Guira Cuckoos preyed on nothing but mice. Carnivorous mammals also fared sumptuously on the rodents. Countless numbers of storks and of short-eared owls came to assist at the general feast, and they became destructive to birds as well as to mice. Diets were changed, habits were changed, numerical proportions were changed, and then the tide turned.

“By August (1873) the owls had vanished, and they had, indeed, good cause for leaving. The winter had been one of continued drought; the dry grass and herbage of the preceding year had been consumed by the cattle and wild animals, or had turned to dust, and, with the disappearance of their food and cover, the mice had ceased to be. In spring it was hard to find a survivor, even in barns and houses. It was pitiful to see the little burrowing owls; for these birds, not having the powerful wings and prescient instincts of the vagrant *Otus brachyotus*, were compelled to face the poverty from which the others escaped. They became tame with hunger, and so reduced as scarcely to be able to fly.”

This is a very instructive case, showing how wave follows wave, how far-reaching the changes they effect may be, and how the waves die away—though not without leaving their mark.

§ 3. REPRODUCTIVE INTER-RELATIONS

When one creature is essential to another for the continuance of its kind we may call this a reproductive inter-relation. Thus the thrush is wrapped up with the continuance of the mistletoe. The berry includes a layer of viscid substance which hardens in air. It is used in making bird-lime. When the thrush eats the berries it rejects the seeds, but these often stick to its bill, and have to be rubbed off against a branch. “The lime sets and the seed is fixed till it germinates, often months later, when in May the temperature is sufficiently high. Professor Keeble tells us of a certain telegraph wire in Ceylon where, yearly,

hundreds of seedlings of an ally of our mistletoe (the tropical *Loranthus loniceroides*) appear where birds have rubbed the seeds from their bills. On the wire, of course, their growth soon comes to an end, but the case is a pretty demonstration of the efficacy of this means of seed distribution and attachment. Seeds may occasionally be eaten by the bird and voided uninjured on a branch, but this is certainly of minor importance in establishing the plant" (Skene, 1921, p. 32).

In some cases the linkage is more at random than in the instance of thrush and mistletoe; yet the results are of much practical importance. A bird often gathers clodlets of earth on its wet feet, and these may contain seeds of plants and germs of animals, which may be washed off again at some distant place. Thus small crustaceans and the like are carried from pool to pool—a fact which is part of the explanation of the uniformity of the minute fauna in widely separated basins. Cases are known where a small freshwater bivalve (*Sphærium*) has clinched its valves on a bird's toe and been transported.

In the "Origin of Species," Darwin gives many examples of the scattering of seeds by fruit-eating birds which often digest the soft parts without injury to the more resistant seeds which pass out of the food-canal none the worse, but he attached much importance to the clodlets on the feet. "The leg of a woodcock was sent to me by a friend, with a little cake of dry earth attached to the shank, weighing only nine grains; and this contained a seed of the toad-rush (*Juncus bufonius*) which germinated and flowered. . . . Professor Newton sent me the leg of a red-legged partridge (*Caccabis rufa*) which had been wounded and could not fly, with a ball of earth adhering to it, and weighing six and a half ounces. The earth had been kept for three years, but when broken, watered, and placed under a bell glass, no less than 82 plants sprung from it; these consisted of 12 monocotyledons, including the common oat, and at least one kind of grass, and of 70 dicotyledons, which consisted, judging from the young leaves, of at least three distinct

species." It is evident, then, that considerable importance may be attached to the fauna and flora of birds' feet.

Another linkage is seen in the pollination of flowers by birds. What insects do as a rule, birds do occasionally. Mr. John H. Lovell (1920, p. 76), writing of North America, says: "Our wild columbine (*Aquilegia canadensis*) has scarlet flowers which are yellow inside, or rarely all over, and is chiefly visited by humming-birds. Other native humming-bird flowers are the cardinal flower, the trumpet-honeysuckle, the painted cup, and the trumpet-flower; but bird-flowers are not common in North America, although abundant in tropical South America."

Mr. Lovell calls attention (1920, p. 136) to the frequent redness of edible berries, and notes that bird-flowers are almost invariably fire-red or scarlet. "In tropical America, where there are more than five hundred species of humming-birds, there are scores of scarlet bird-flowers, such as scarlet sages, fuchsias, and abutilons; while in Europe, as Kerner points out, where neither the humming-birds of America nor the sun-birds of Africa nor the honeysuckers of Australia are found, scarlet blossoms are noticeably absent. It is difficult not to believe that anthophilous birds have learned to associate bright red colours with the presence of an ample food-supply of nectar and small insects."

§ 4. PARASITES OF BIRDS

Like other animals, birds have a large number of parasitic retainers, varying from microscopic blood-parasites to long tapeworms. Some of these parasites keep to the outer surface, and work hard among the feathers and scales, especially when these become foul or when the bird gets out of condition. The most important of these ectoparasites are (1) the biting-lice or Mallophaga which feed on the delicate portions of the feathers; (2) the unrelated true lice (belonging to the order Hemiptera) which suck blood; and (3) the skin-mites and scale-mites which are

not insects at all but belong to the Acarine order of Arachnids.

Apart from microscopic Protozoa, the endoparasites of birds are chiefly "worms." There are (1) flukes or Trematodes, *e.g.* *Distomum macrostomum* in various perching birds; (2) tapeworms or Cestodes, *e.g.* *Tœnia anatina* in the duck; and (3) threadworms or Nematodes, *e.g.* *Trichostrongylus pergracilis* of the grouse. The three examples mentioned all live in the food-canal, but other organs of the bird's body may be affected.

Some species of parasites occur in several different kinds of birds, but in many cases a particular parasite is peculiar to a particular kind of bird. The discovery of a new bird usually means the discovery of new parasites. This may illustrate the establishment of new species in isolated habitats, for each kind of bird is in a way like an island. Its parasites are linked to it and adapted to it, and cannot readily pass to a different kind of bird. But the question rises insistently whether many of these so-called species are more than different modifications of one species. Crucial experiments are much needed.

Linked by a Common Parasite.—Many parasitic worms require two hosts, one for their juvenile and asexual stages, another for the full-grown and sexually reproductive forms. Thus the young of the liver-fluke of the sheep lives in the little freshwater snail, and the bladderworms of the pig and the ox become tapeworms in man. Similarly, there are certain flukes and tapeworms which occur as adults in birds, while the young stages live in fishes which form a normal part of the birds' diet. It seems that some of the pearls found in bivalves are formed round the larvæ of parasitic worms whose adult stages occur in mollusc-eating birds.

§ 5. STRANGE LINKAGES

As an example of the quaint linkages that sometimes occur, we may take the partnership between the Crocodile

of the Nile and the Crocodile Bird or Trochilus, which Herodotus described long ago. Various naturalists, such as the elder Geoffroy Saint-Hilaire and A. E. Brehm have observed the strange partnership and seen the bird, *Pluvianus ægyptius*, a kind of plover, enter the reptile's mouth, probably to pick off leeches or some morsel of food. It often rests on the crocodile's back and in addition to its cleansing offices it may be of service as a sentinel. For the crocodile is usually a timid animal as far as man is concerned. Brehm says of the bird: "Observant, inquisitive, excitable, clamorous, and gifted with a far-reaching voice, it is well fitted to serve as watchman to all less careful creatures. No approach, whether of beast of prey or of man, escapes its suspicious observation; every sailing-boat or rowing-boat on the river attracts its attention; and it never fails to tell of its discovery in loud cries. Thus it brings under the notice of all the other creatures who share its home or resting-place the unusual occurrence, enabling them either to find out for themselves if there is really any danger, or to make good their escape on the strength of its warning. Thus it discharges the duties of a sentinel. Its friendly relations with the crocodile can hardly be called mutual, for to credit the crocodile with friendship is going rather far. Certainly the reptile treats the bird as a harmless creature, but this is not out of any benevolence, but simply because he has a thorough knowledge and a correct estimate of his partner" ("From North Pole to Equator," Trans., 1896, p. 227).

A. Leith Adams has an interesting note in this connection. "A sail, or the smoke and noise of a steamboat, suffice to warn the crocodiles basking on the sand-banks, or their common companions, the black-headed and spur-winged plovers (*Pluvianus ægyptius* and *Hoplopterus spinosus*), which are frequently seen perched upon their backs, and always prepared to give timely warning of approaching danger, just as the Father of History noticed them 2,300 years ago, and, strange to say, his well-known story is current among the modern Egyptians, who, as usual, have

put a tail to the narrative. They say, that in addition to its office of leech-catcher to the crocodile, it occasionally does happen that the zic-zac—so called from its note of alarm—in searching for the leeches, finds its way into the reptile's mouth when the latter is basking on a sand-bank, where it lies generally with its jaws wide apart. Now this is possible and likely enough, but the captain of our boat added, that occasionally the crocodile falls asleep, when the jaws suddenly fall, and the zic-zac is shut up in the mouth, when it immediately prods the crocodile with its horny spurs, as if refreshing the memory of his reptilian majesty, who opens his jaws and sets his favourite leech-catcher at liberty" ("Notes of a Naturalist in the Nile Valley and Malta," 1870).

§ 6. THE HAND OF MAN ON BIRDS

When prehistoric man found his way to Scotland, perhaps ten thousand years ago, the country was recovering from the Great Ice Age which had killed off almost every living creature. For many years the country had been in process of restocking by animal-immigrants from the South of England, and from what, in our insulation, we now call the Continent. Scotland was then a smaller country than it is to-day, for the sea stood at the level of "the Fifty-Foot Beach" and the estuaries reached far inland. "It was a country," we read, "of swamps, low forests of birch, alder, and willow, fertile meadows and snow-clad mountains," into which Neolithic Man penetrated—a "long-headed, square-jawed, short, but agile-limbed, hunter and fisherman. There were no domesticated animals in those days, nor any dubious aliens like rabbits and rats. But there were elk and reindeer, wild cattle, wild boar, perhaps wild horses, a fauna of large animals on which lynx, brown bear, and wolves levied toll. In all likelihood, the marshes resounded to the boom of the bittern, and the plains to the breeding-calls of the crane and the great bustard."

This post-glacial fauna affords a good starting-point for an inquiry into the effect of man's hand upon animal life, and this inquiry has been conducted in a masterly way by Dr. James Ritchie in his great book, "The Influence of Man on Animal Life in Scotland" (1920). The post-glacial fauna was the capital with which prehistoric man started, to which he added various acquisitions from abroad, and into which, at times, he dipped heavily. What were the changes as far as birds are concerned?

Among deliberate changes, the first place must be given to domestication, which included poultry and pigeons. The direct effects on the structures and functions, habits and temperaments of the animals domesticated (*e.g.* horse and cattle, sheep and dog) were so great that man's rôle became almost like that of a creator, though in actual fact he has never done more than sift and shuffle the novelties which creative evolution supplies. Domesticated birds shared in this transforming. But to feed and protect his stock man operated largely on the country, and this brought about far-reaching changes, which affected wild birds as well as wild beasts.

But domestication almost necessarily leads to a destruction of wild life, for although flocks and herds lighten the earlier task of hunting for food, there rises a new need for restricting the enemies of the domesticated stocks. The larger carnivores are hunted down, and such fine birds as eagles. There is a persecution of the smaller beasts of prey, such as wild cat, polecat, and pine-marten, and of hawks and owls. The regret is not only scientific and æsthetic, but economic as well, for the destruction of the carnivore means the increase of the rodent; and the multiplication of rats and mice and voles involves losses which have to be set against the increased safety of, let us say, the poultry yard.

In old days many wild birds were killed for food, and on the Baltic shores to-day we may see the salting of barrel-fuls of crows. Other birds were used for their fat and feathers, and so forth, and a distinction must be drawn

between exploitation for utility and elimination for "fun," or greed, or a mania for possessing. A caged songster is a sad sight and a basketful of dead larks is sadder still; but neither is so deplorable as killing birds for fun. But it is not always easy for even the humanitarian ornithologist to keep his hands quite clean.

As an offset to deliberate destruction, which our ancestors practised for utility and our contemporaries for sport, there is deliberate protection. This is to a slight extent rooted in superstition (of a type not to be much deplored), as may be seen in the respect paid to robin and wren, spider and lady-bird. It is also in some measure due to sincere popular favour (long may it flourish and widely may it spread!) as we see in the goodwill that shelters cuckoo and nightingale, and many another bird. But protection is chiefly to the credit of "the law," and, as Dr. Ritchie points out in the book we are following, this has had an interesting evolution. It was at first almost wholly an aristocratic method of protecting wild animals for sport purposes; the basis broadened, however, and all sorts of useful animals and birds were included; of recent years there have been welcome hints of a new sense of values, for the ægis of the law is being extended to the beautiful.

Besides domestication, destruction, and protection there has been another deliberate action on man's part, namely, the introduction of new animals from other countries. In many cases this has been followed by results as far-reaching as they were unexpected, and the well-known consequences of introducing rabbits into Australia are paralleled by those which followed the repeated importation of European sparrows to the United States. About 1,500 sparrows were introduced in North America between 1850 and 1870, partly in the hope that they would check the ravages of the elm-tree caterpillar, for sparrows feed their young ones on caterpillars.

"To these introduced birds," Professor H. C. Bumpus wrote in 1898 ("Wood's Holl Biological Lectures," 1896-1897, pp. 1-15), "the environment has been novel. They

have found abundant food, convenient and safe nesting places, practically no natural enemies, and unrivalled means of dispersal. Aside from an early and brief period of fostering care, they have been left to shift for themselves ; natural agencies have since been at work, and in the relatively short space of forty years a continent has been, not merely invaded, but inundated by an animal which, in its native habitat, has been fairly subservient to the regulations imposed by competing life."

Biologically regarded, this is an interesting instance of the practical suspension of the sifting operations of Natural Selection, but also of the results of rapidly altering the moving equilibrium of Nature. The sparrows multiplied exceedingly. In some measure, it is true, they checked the elm-tree caterpillars, but only to become themselves a greater pest. They did great damage to the crops, including buds, they drove away native insectivorous birds, and they are blamed for spreading among poultry certain diseases, such as "blackhead," due to parasitic *Coccidia*. They often became a nuisance about houses. What has happened in the past goes on to-day, for no successful method of checking or exterminating sparrows has been discovered. In his "Economic Zoology" (Philadelphia, 1919), Professor A. M. Reese notes that, according to some computations, 98 per cent. of the sparrow's food is vegetable and 74 per cent. of this is grain of some sort. "It is of some slight value about towns as a scavenger and possibly does some good as a destroyer of insects and weed seeds, but the total balance seems to be strongly against it."

Apart from domesticated forms, man has introduced into Britain the pheasant, the red-legged partridge, the capercaillie, and a number of other birds.

Man's hand is often heavier indirectly than directly. The destruction of the Scottish forests has changed the whole face of the country, and deprived many birds of their old homes ; drainage has driven marsh birds away ; and the extension of agricultural ground has meant a great reduction of the wild places that afford shelter to nests.

These things must be, and the only remedy is in the conservation of sanctuaries and in the diffusion of a reluctance to kill needlessly.

When we take a country like Scotland, which is peculiarly well-adapted for precise faunistic study, we find, following Dr. Ritchie, that more species of animals have been introduced than have been exterminated since man entered into his Scottish kingdom. This seems at first sight very satisfactory, but it is not the whole truth, for while the fauna has actually gained in numerical strength it has fallen off in what we might call faunistic value or standard. The visible has been replaced by the invisible, the giants by the pigmies. "We have, in effect, lost more than we have gained, for how can increase of rabbits and sparrows and earthworms and caterpillars, and the addition of millions of rats and cockroaches and crickets and bugs, ever take the place of those fine creatures round the memories of which the glamour of Scotland's past still plays—the reindeer and the elk, the wolf, the brown bear, the lynx, and the beaver, the bustard, the crane, the bumbling bittern, and many another, lost or disappearing?"

In the 1903 British Museum Report on Economic Zoology, Sir Ray Lankester has clearly arranged the chief practical inter-relations between man and animals. We wish to illustrate his categories with reference to birds in particular.

(1) Birds captured for food and other products, *e.g.* crows salted in barrels in some parts of North Europe; ptarmigan, willow grouse, plover, woodcock, snipe, wild duck, etc., shot and trapped for food.

Here may be included wild birds like Red Grouse and Partridge shot rather for sport than for food. And another sub-category of a more dubious character may be recognised for birds that are killed for purposes of luxury, *e.g.* those male Birds of Paradise that are shot for the sake of their very decorative feathers.

(2) Birds bred for use, such as poultry for food, ostriches for their plumes, pheasants for sport, carrier-pigeons for sending news.

(3) Birds that help man's operations, more or less directly ; thus some small birds pollinate flowers and some distribute useful plants, many like gulls and kites are very useful scavengers.

(4) Birds that hinder man's operations. This must be a very short list, restricted to a few cases like aggressive ostriches.

(5) Birds that injure useful animals and plants, *e.g.* house sparrows which spoil crops and drive away insectivorous birds ; wood-pigeons which eat enormous quantities of grain ; herring-gulls when they become very vegetarian and destroy full-grown turnips and the ears of corn in the sheaves ; the kea-parrot that kills sheep in New Zealand.

(6) Birds that spoil or destroy man's permanent products, *e.g.* house-sparrows which sometimes make an ivy-covered house intolerably dirty ; starlings in so far as they do damage in a farm-steading.

(7) Birds that keep a check on creatures (*a*) that hinder man directly, (*b*) that injure useful animals and plants, and (*c*) that spoil or destroy man's permanent products.

Thus (*a*) some birds destroy snakes, others rats, others mosquitoes.

(*b*) Others check the increase of voles and sparrows, plant-lice and scale-insects.

(*c*) Others check various injurious insects that destroy man's permanent products.

The uses of birds are much more *varied* than one might think, and we take a few illustrations from an interesting lecture by Mr. Hugh S. Gladstone (1920). Canaries, being about fifteen times more sensitive than man to poisonous gases are used in this connection in mines and were used in the war. . . . In 1910 about £1,500,000 worth of ostrich feathers were imported into Great Britain, in 1919 more than £30,000,000 worth of eggs and poultry. Some domestic strains of poultry are veritable egg machines, laying as many as 3000 eggs in a lifetime, whereas the original Jungle Fowl in a wild state lays at the utmost forty or fifty. . . . " After the conquest of Gaul relays of pigeons carried

the news to Rome, as, in later days, the news of the victory at Waterloo was brought to England by pigeons some days in advance of the official courier." . . . Penguin oil from the Falkland Islands has a more than local utilisation. . . . The sinews of birds are used by certain remote tribes in place of thread. . . . But the *indirect* utility of birds, especially in keeping down injurious insects, is much more important than the direct utility. As Michelet tersely put it: "L'oiseau peut vivre sans l'homme, mais l'homme ne peut vivre sans l'oiseau."

§ 7. THE INTER-LINKING OF LIVES

The main theme of this chapter—the intricate inter-linking of lives—may be illustrated by Dr. Ritchie's story of the Black-headed Gulls on the White Moss, near West Linton, in Peeblesshire. In 1890 it was a typical heather moor, with peat and moisture underneath. In 1892 or 1893 a few pairs of gulls came to nest on the Moss, and were encouraged; in 1897 there was a populous colony; in 1904 the number was estimated at 1,500 to 2,000 pairs. The vegetation round about underwent a remarkable change; the heather was replaced by coarse grass, that by rushes, and these, again, by a forest of docks.

These changes were partly due to the fertilising of the soil by food-refuse and excreta from the gullery, and partly to the puddling of the surface by the thousands of feet and to the surface accumulation of the crowded nests, "so that superficial water was retained, and the peat bed with concealed and deep moisture was transformed into a surface marsh."

But more changes were in process. The grouse disappeared from the moor and teal ducks came, attracted by the marsh and the rushes. A single flock, with as many as seventy ducks, was seen when the gullery was at its height.

Fifteen years passed, and man interfered again, rapidly ousting the gulls from their tenancy of the White Moss.

The villagers were disappointed because the coarse grass they used to cut had been replaced by docks, and the proprietor, who had been using a percentage of gulls' eggs as food for his young pheasants, was disappointed, because the grouse had gone. In the early summer of 1917 scarcely a gull was to be seen; the docks had almost disappeared; the rushes were giving way to rough grasses and even heather; the teal had gone and the grouse were returning.

We see, then, how in a few years a slight imprint of man's hand had set in motion a complicated cycle of changes, and there is something almost startlingly reminiscent of Darwin in the last sentence of Dr. Ritchie's story: "If the natural processes set a-rolling by a tiny and temporary interference of man can be so marked, how can imagination grasp the total effects of man's influence, impressed upon the world of Nature often with great power, and persisted in, not for a few years, nor for a few centuries, but for thousands, nay, even for tens of thousands of years."

§ 8. THE CONSERVATION OF BIRDS

From the instances that we have given—samples out of many—it seems clear that science warrants the strongest disapprobation of the careless destruction of birds. Some have calculated that six to ten years without birds would serve to bring our whole system of Animate Nature to an end. The accuracy of such statements cannot be demonstrated, and they are better left alone. What is certain is that the continuance of the system of Animate Nature depends in part on the check that birds keep on injurious insects and on small mammals like voles. There is a *very* short list of birds that are seriously injurious to the interests of farmer and gardener; of a considerable number it must be said that while they do harm they also do good, and that the balance is greatly in their favour; of the vast majority it may be safely said that they are beneficial.

They are "joys for ever besides," and this is a note which should be sounded along with that of utility. These birds

are the masterpieces of ages, they are "fearfully and wonderfully made," they are beautiful and charming personalities, and, once gone, they are irreplaceable. All the king's horses and all the king's men cannot give us back an exterminated Dartford Warbler. In abetting the destruction of treasures of which we are the responsible trustees, we are not only impoverishing the fauna, but doing violence to our own better selves.

We welcome such a wise measure as the Plumage Bill, but there is still great need for an education of public opinion in regard to the conservation of birds. The backwardness is due, we are convinced, rather to lack of attention and imagination than to lack of good-will. Let us take an appeal from one of Mr. W. H. Hudson's unsurpassable essays, where he is describing the American ostrich or Rhea, notable for its fleetness, great staying powers, and beautiful strategy when hunted, and for its strange habit of "running with one wing raised vertically, like a great sail—a veritable ship of the wilderness."

"Rhea-hunting, the 'wild mirth of the desert,' which the native horseman has known for the last three centuries, is now passing away, for the Rhea's fleetness can no longer avail him. He may scorn the horse and his rider, what time he lifts himself up, but the cowardly murderous methods of science, and a systematic war of extermination, have left him no chance. And with the Rhea go the flamingo, antique and splendid, and the swans in their bridal plumage, and the rufous tinamou—sweet and mournful melodist of the eventide; and the noble crested screamer, that clarion-voiced watch-bird of the night in the wilderness. These, and the other large avians, together with the finest of the mammalians, will shortly be lost to the pampas as utterly as the great bustard is to England, and as the wild turkey and bison and many other species will shortly be lost to North America. Like immortal flowers they have drifted down to us on the ocean of time, and their strangeness and beauty bring to our imaginations a dream and a picture of that unknown world immeasurably far removed."

No doubt there are signs of a reaction against submitting to an impoverishment of Animate Nature, but there is much to be done. We should try to secure the conservation of more tracts of country in which waning forms of life may be fostered. We should raise a prejudice against "big bags" and *ruthless wasteful* sport which defeats its own ends. We should abstain from all products which mean the extinction of fine types. We should try to appreciate the seriousness of impending losses, not only in their economic, but in their scientific and æsthetic aspects.

As on another occasion (1917, p. 124) we conclude by quoting Ruskin's translation of what Socrates said in regard to the halcyon, for it is suggestive of the mood in which we do well to consider these things.

"*Chærophon* : And is that indeed the halcyon's cry ? I never heard it yet ; and in truth it is very pitiful. How large is the bird, Socrates ?

"*Socrates* : Not great ; but it has received great honour from the gods, because of its lovingness ; for while it is making its nest, all the world has the happy days which we call halcyonidæ, excelling all others in their calmness, though in the midst of storm.

" We being altogether mortal and mean, and neither able to see clearly great things nor small, and for the most part being unable to help ourselves even in our calamities, what can we have to say about the powers of the immortals, either over halcyons or nightingales ? But the fame of fable, such as our fathers gave it to us, this to my children, O thou bird singing of sorrow, I will deliver concerning thy hymns ; and I myself will sing often of this religious and human love of thine, and of the honour thou hast for it from the Gods.

"*Chærophon* : It is rightly due indeed, O Socrates, for there is a twofold comfort in this, both for men and women, in their relations with each other.

"*Socrates* : Shall we not then salute the halcyon, and so go back to the city by the sands, for it is time ? "



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